Ecological applications of imaging spectroscopy in alpine grasslands

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Front page: Val Trupchun in the Swiss National Park (Photo: © Christian Schmid)

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SUMMARY

Ecosystem ecology investigates the processes driving ecosystems, the services ecosystems provide and how these processes and services are linked to the organism community. However, due to the complexity of ecosystems and an inherent multitude of interactions, the links between ecosystem processes and services and the organism community are only partly understood.

The vegetation community serves as an indicator for various ecosystem processes and services, as plants integrate synergistic as well as antagonistic environmental factors over space and time and are relatively easy observable. However, vegetation surveys are time consuming and require area-specific expert knowledge and are thus usually limited to small research plots located within limited geographic areas. In alpine grasslands, high heterogeneity and diversity, together with restricted accessibility and sensibility to disturbance, pose additional challenges for traditional vegetation ecology studies.

In the face of global change, there is an increasing demand for continuous and large scale vegetation data to enable coherent ecosystem assessment. Remote sensing enables collecting such continuous data over large, heterogeneous and poorly accessible areas within short periods of time. Imaging spectroscopy is particularly useful in vegetation ecology, as the spectral response provides detailed information on the structural and biochemical characteristics of the material measured. Moreover, current developments are directed towards increasing the spatial and spectral resolution of sensors and scaling their application from field measurements to regions covered by airborne and spaceborne sensors.

Thus, establishing the causal links between the spectral response of the vegetation, plant structural, biochemical and functional traits, trait diversity and the ecological relevance of these traits provides the opportunity to bring ecosystem ecology to the landscape and global level. Together with assessing the consequences of altering trait abundances, these links can be used to address today´s most challenging environmental issues, such as resource exploitation and changes to biogeochemical cycles.

This thesis introduces a common framework for merging the theory and concepts of imaging spectroscopy and vegetation ecology. Furthermore, it illustrates how imaging spectroscopy and vegetation data can be combined to successfully model, predict and map a series of vegetation community traits, i.e. plant biomass, plant nitrogen and fibre content, plant life and growth forms, strategy types and indicator values. According to our results, a sampling design covering the entire expected heterogeneity of the research area and validation data sets enabling to assess model plausibility and transferability between sites and scales seems highly advantageous. The application of vegetation quantity and quality maps for the analysis of animal movement patterns shows how imaging spectroscopy can be used to gain additional insights into a classic ecological question, i.e. resource partitioning within an animal guild. In summary, the results and products of this thesis, high resolution maps of vegetation community traits, provide the basis for assessing and monitoring ecosystem processes and species distributions in a strictly protected and highly diverse alpine ecosystem, the Swiss National Park (SNP).

ZUSAMMENFASSUNG

Die Ökosystem-Ökologie untersucht das Wirkungsgefüge von Organismengemeinschaften, Ökosystemprozessen und -dienstleistungen. Diese Wechselwirkungen sind auf Grund der vielen beteiligten Faktoren und der dadurch komplexen Interaktionen nur schwer im Einzelnen zu fassen.

Vegetationsgemeinschaften können als Indikatoren für Ökosystemprozesse und -dienstleistungen dienen, da Pflanzen sowohl synergistische als auch antagonistische Ökosystemprozesse auf räumlicher und zeitlicher Ebene integrieren und zudem relativ einfach zu beobachten sind. Botanische Aufnahmen sind allerdings zeitaufwendig und benötigen standortspezifische Artenkenntnis, weshalb sie meist auf einzelne Probeflächen eines kleinen Gebiets begrenzt sind. Alpine Graslandschaften zeichnen sich zudem durch grosse Heterogenität und Diversität aus, sind oft nur schwer zugänglich und können mitunter sehr sensibel auf Störungen reagieren, was eine zusätzliche Herausforderung für traditionelle vegetationsökologische Feldaufnahmen darstellt.

Angesicht des globalen Wandels bedarf es allerdings flächendeckender und grossräumiger Datensätze, um Ökosystemprozesse und die von ihnen bereitgestellten Dienstleistungen vergleichbar zu beurteilen. Fernerkundungsmethoden ermöglichen es, solche flächendeckenden Daten selbst in heterogenen und schwer zugänglichen Gebieten innerhalb kurzer Zeit zu erfassen. Das spektrale Signal von Bildspektrometern ergibt sich aus den strukturellen und biochemischen Eigenschaften der gemessenen Substanz, weshalb sich diese Methode besonders gut für die vegetationsökologische Forschung eignet. Laufende Entwicklungen im Bereich von Bildspektrometern zielen ausserdem auf die Erhöhung der räumlichen und spektralen Auflösung, sowie auf ihre Implementierung in Luftbild- und Satellitensysteme ab.

Die Herstellung kausaler Verbindungen zwischen dem spektralen Signal der Vegetation und den strukturellen, biochemischen und funktionellen Pflanzeneigenschaften, deren Verteilung und Relevanz, sowie der Konsequenzen einer Veränderung dieser Eigenschaften, ermöglicht es daher, Ökosystem-Ökologie auf die landschaftliche und globale Ebene auszuweiten. Somit werden die Voraussetzungen geschaffen, um grossen aktuellen Umweltproblemen, wie der Ausbeutung von Ressourcen und der Veränderung des biogeochemischen Kreislaufs, wirkungsvoll entgegenzutreten.

Die vorliegende Arbeit verknüpft die Theorien und Konzepte von Bildspektrometrie und Vegetationsökologie und fasst sie in einen gemeinsamen Rahmen. Wir zeigen, wie Biomasse, Stickstoff- und Fasergehalt der Vegetation, sowie verschiedene funktionelle Pflanzentypen (Lebensformen, Wuchsformen, Strategietypen und Indikatoren), durch die Kombination von Bildspektrometrie- und Vegetationsdaten, erfolgreich modelliert, vorhergesagt und kartiert werden können. Dabei erwiesen sich Bodendaten, welche die gesamte zu erwartende Heterogenität der Vegetation abdecken, als überaus vorteilhaft. Zusätzliche Validierungsdaten ermöglichten es, die Plausibilität und Übertragbarkeit der Modelle zu überprüfen. Die Analyse von Tierbewegungsmustern veranschaulicht, wie Karten zur Vegetationsquantität und -qualität angewandt werden können, um zusätzliche Einblicke in eine klassische ökologische

Fragestellung, die Ressourcenaufteilung innerhalb einer Artengemeinschaft, zu gewinnen. Die hochauflösenden Karten funktioneller Vegetationseigenschaften des alpinen Graslands, die im Rahmen dieser Arbeit erstellt wurden, dienen als Grundlage zur Untersuchung einer Vielzahl von Ökosystemprozessen, sowie der Verbreitungsmuster verschiedener Arten im streng geschützten, hochdiversen, alpinen Ökosystems des Schweizerischen Nationalparks (SNP).

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1 INTRODUCTION

Grasslands are spatially and temporally heterogeneous landscape elements supporting highly diverse species communities (Wilson *et al.* 2012) and provide a multitude of ecosystem services (Sala & Paruelo 1997). Ecosystem services summarize the benefits humans obtain from ecosystems, including i) provisioning services, such as soil fertility and water availability, ii) regulating services affecting climate, nutrient cycling, resistance to and resilience after disturbance, iii) cultural services providing recreational and spiritual benefits, and iv) supporting services maintaining, for example, soil formation and photosynthesis (MEA 2005). Assessing ecosystem services and predicting trends for the future are essential for the conservation of natural resources, sustainable development and human well-being. Ecosystem services are provided by populations of organisms (MEA 2005), therefore the composition and abundance of biological units (biomes, species and populations) serve as indicators for ecosystem service assessment.

Plants integrate the environmental factors relevant for their development over space and over time. Depending on synergistic as well as antagonistic effects of (micro-)climate, soil and disturbances (Hooper & Vitousek 1997), plants make use of biophysical and biochemical resources, and allocate the energy gained towards growth, seed production and protective structures. Constantly trading-off energy investments, plants indicate subtle abiotic and biotic environmental conditions, giving more reliable information than punctual measurements of single biophysical or biochemical ecosystem characteristics (Zonneveld 1983). Moreover, the heterogeneity of grasslands limits the ability of traditional systematic field surveys to assess ecosystem characteristics and community composition. Detailed vegetation surveys, including the mapping of species composition or plant functional types (PFTs), remain often limited to small areas or broad classification schemes, as extrapolations of field data are often not reliable.

Remote sensing provides the only realistic means to acquire standardized and detailed environmental data over large areas, at a high enough spatial and temporal resolution to develop globally consistent ecosystem service assessment and monitoring schemes (Kerr & Ostrovsky 2003). Particularly, imaging spectroscopy is extremely valuable for ecological studies as it collects the reflectance characteristics of materials, such as the vegetation, in more than a hundred spectral channels (Goetz *et al.* 1985) indicating subtle differences in its structural and chemical composition (Aplin 2005). While the theory of imaging spectroscopy is well established, the instruments capable of delivering reliable measurements are just being developed. The research presented in this thesis builds upon data from the airborne imaging spectrometer APEX (airborne prism experiment; Schaepman *et al.* 2015) and field data from vegetation plots to predict and map an array of vegetation traits in highly heterogeneous alpine grassland and provides examples for the application of the resulting products in vegetation and animal ecology.

This introductory chapter briefly describes some general properties of grasslands (section 1.1), introduces the basic theory of imaging spectroscopy (section 1.2) and vegetation mapping (section 1.3), before defining the research context (section 1.4), the main research questions (section 1.5) and the structure of the thesis (section 1.6).

1.1 Grasslands

Grasslands are generally defined as the physiognomic vegetation unit (the vegetation formation) dominated by grasses (van der Maarel 2005). About 25% of the Earth's land surface (approximately 34 000 000 km^2 of 146 000 000 km^2) is covered by grasslands, including savannah and mixed types of cropland and natural vegetation (Loveland *et al.* 2000). Open landscapes have already been important for our ancestors as they, in contrast to forested areas, provided overview over large areas, orientation possibilities and ease of movement. The diverse plant and animal communities of grasslands, particularly medium to large sized herbivores, offered favourable conditions for hunting and gathering, as well as for establishing semi-permanent and permanent settlements. In fact, the majority of domesticated plants and animals originated from grasslands (Sala & Paruelo 1997). Humans have influenced almost all grassland ecosystems, increasing their extent during the Holocene (the past 11 600 years) by about 10 000 000 km^2 or 7% of the total global land cover (Loveland *et al.* 2000; Lemmen 2010). Today, depending on water availability and the amount of agricultural subsidies distributed, most of the world's grasslands are intensively used (Sala & Paruelo 1997). Thus, the economic value of grasslands is usually quantified in the amounts of crop, milk, meat, leather or wool produced (Sala & Paruelo 1997). However, semi-natural grasslands, such as alpine grasslands, provide a vast array of ecosystem services, including climate control, genetic resources, soil and water protection (Harrison *et al.* 2010) with quantifiable values comparable to or greater than the direct revenues of agricultural products on the marked (Sala & Paruelo 1997). Ecosystem service assessment acknowledges these non-market values (Schägner *et al.* 2013) of grasslands and points out the need for consistent assessment and monitoring schemes, especially in the course of global change (MEA 2005).

The vegetation occurring in the alpine zone, i.e. between sub-alpine forest and the nival zone dominated by permanent snow cover, is commonly referred to as 'grassland'. However, as alpine grasslands can be dominated by a mixture of grasses and forbs or a mixture of grasses, forbs and dwarf shrubs, the vegetation unit has also been referred to as 'alpine meadow' (e.g. Jaeger III *et al.* 1999; Bowman *et al.* 2006) or 'alpine tundra' (e.g. Bowman *et al.* 1993; Choler *et al.* 2001; Baptist *et al.* 2010). When the vegetation is short with considerable amounts of open soil, the term 'alpine steppe' is equally valid (e.g. Meyer & Thaler 1995; Schönswetter *et al.* 2005). Throughout this thesis, we use the terms 'grassland' for non-forested vegetation in the alpine zone and 'meadow' for non-forested vegetation with apparent influences of human land use in the sub-alpine zone, irrespective of vegetation height and the dominance of grasses, forbs and dwarf shrubs.

1.2 Imaging spectroscopy

The science of spectroscopy studies electromagnetic radiation (ER) as a function of wavelength that has been emitted, reflected or scattered from a solid, liquid or gas (Clark 1999). Imaging spectroscopy measures the ER in calibrated radiance units ($L = W\ m^{-2}\ sr^{-1}\ nm^{-1}$) by simultaneously collecting spatially co-registered images, in many narrow, spectrally contiguous bands, from a remotely operated platform (Schaepman *et al.* 2006). The data produced is called 'imaging spectroscopy data'. Imaging spectrometry, in contrast, is the engineering task of defining and building the instrument and the science of making imaging spectroscopy data available.

The electromagnetic spectrum ranges from high frequency, high energy, short wavelength Gamma rays, to low frequency, low energy, long wavelength radio waves (Fig. 1.1).

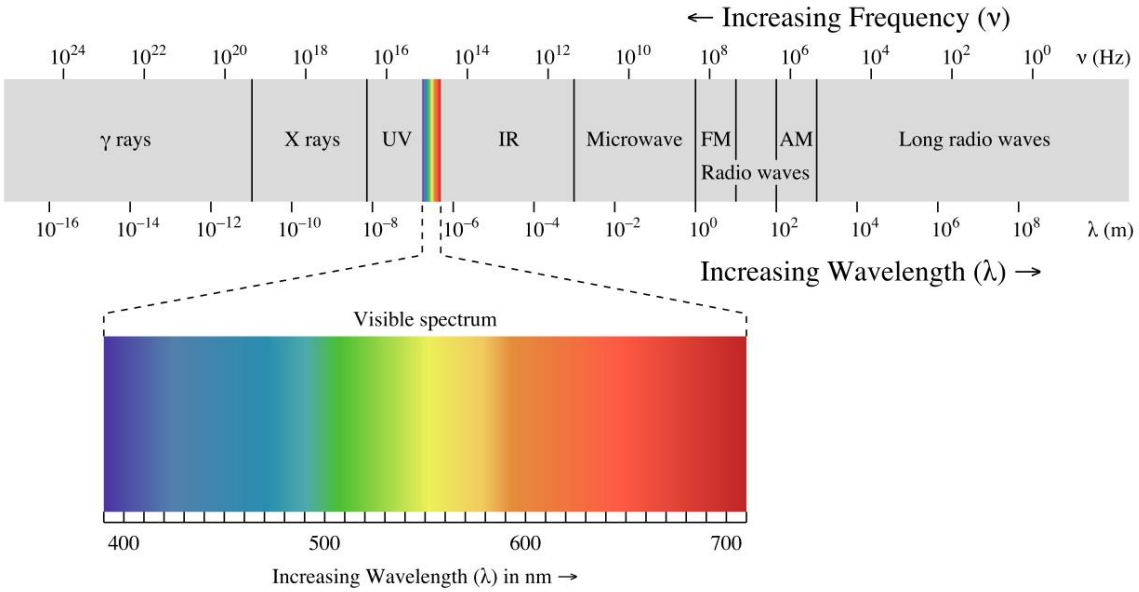


Figure 1.1 The electromagnetic spectrum (Ronan 2007).

The sun emits ER predominantly in wavelengths between 200 nm and 2500 nm with a peak around 500 nm and a distribution that, according to Planck's law, approximates a black body (Ollinger 2011) at 5500 °C, which is approximately the effective temperature of the solar atmosphere (5778 K; Fig. 1.2; Williams 2013). About half of the electromagnetic energy reaches the Earth's surface in the visible part of the spectrum (VIS; c. 400–700 nm), the remaining half in the ultraviolet (UV; c. 250–400 nm), near-infrared (NIR; c. 700–1000 nm) and short-wavelength infrared (SWIR; c. 1000–4000 nm; Jones & Vaughan 2010). In the atmosphere, ER is scattered by dust, atmospheric molecules and aerosols and absorbed at various wavelengths by different gases with specific absorption bands (Fig. 1.2; Jones & Vaughan 2010).

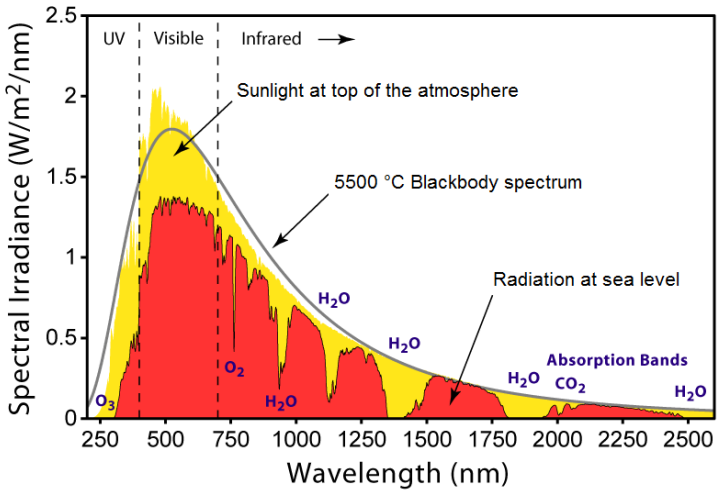


Figure 1.2 Solar irradiance (sunlight) at the top of the Earth's atmosphere (yellow) and at sea level (red). The curves are based on terrestrial reference spectra from the American Society for Testing and Materials (ASTM), regions for ultraviolet (UV), visible and infrared light are indicated (modified after Rohde 2007).

While most of the ER in the UV is absorbed by ozone (O_3) and oxygen (O_2), far less is absorbed in the VIS. In the NIR and SWIR water vapour (H_2O) and carbon dioxide (CO_2) form major absorption bands (Fig. 1.2; van der Meer *et al.* 2009). The transparent regions of the atmosphere where electromagnetic radiation can reach the Earth's surface are called atmospheric windows (red areas in Fig. 1.2).
Laboratory, hand-held, airborne and spaceborne spectrometers remotely detect the reflection of light in many narrow bands, typically from the VIS to the SWIR part of the spectrum. In contrast to photo cameras, usually providing spectral information in three bands, one in the red, one in the green and one in the blue part of the spectrum, imaging spectrometers record the reflectance, for example, in 100 bands in the red, 100 in the green, 100 in the blue and 100 in the NIR and SWIR (Fig. 1.3).

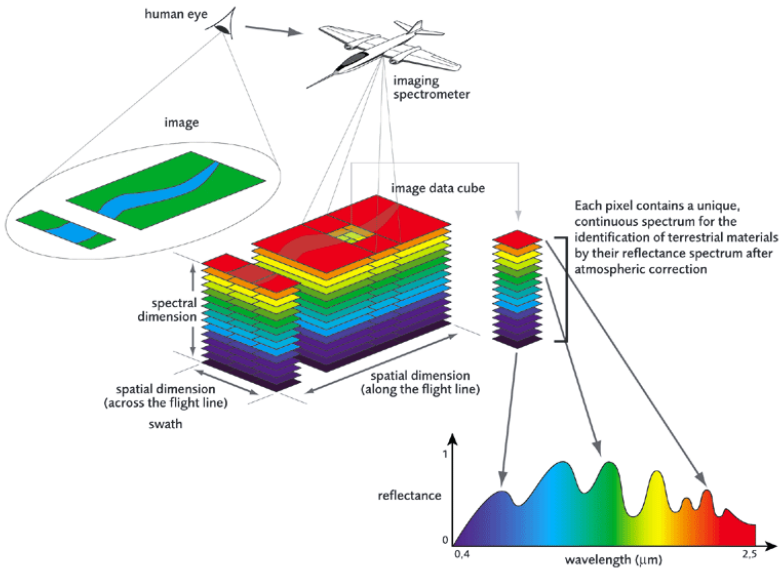


Figure.1.3 The principle of imaging spectroscopy (Schweiger *et al.* 2013; modified after Vane & Goetz 1988).

The shape of the spectrum, also called the reflectance curve, depends on the structural and biochemical characteristics of the material measured (Ustin *et al.* 2004). The reflectance in the VIS part of the spectrum is predominantly determined by electronic transitions. Atoms and ions with discrete energy states absorb photons in specific wavelengths, causing them to change from one energy state to a higher one. As they return to their original state, heat or fluorescence gets emitted and the energy that was gained can be coupled to chemical reactions, such as photosynthesis. In the NIR and SWIR part of the spectrum ER influences vibrational and rotational frequencies in molecules (Ollinger 2011), which depend on the masses of the elements involved and the strength of the molecule bonds.
The energy per quantum of light declines from shorter to longer wavelengths, thus photosynthetically active plants predominantly absorb narrower, more energetic wavelengths in the VIS (photosynthetically active radiation (PAR)), with major pigment absorption features in the red and blue and less absorption in the green parts of the spectrum (Fig. 1.4.). In contrast, the energy level in the NIR is not high enough to drive photosynthesis, but could cause overheating and damage to plant tissues and thus gets predominantly scattered and reflected (Fig. 1.4; Jones & Vaughan 2010).

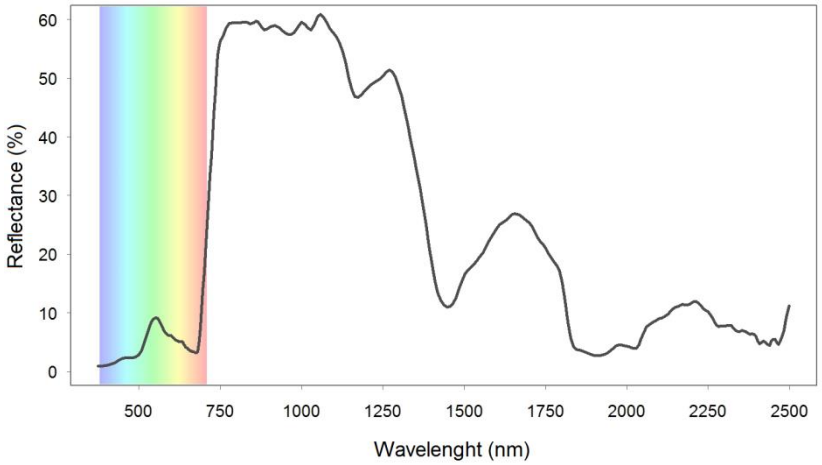


Figure 1.4 Reflectance spectrum of vegetation and photosynthetically active vegetation (PAR). The visible part of the spectrum is indicated in blue-green-red, where PAR is absorbed (400–700 nm).

Life on Earth depends on organisms that are able to transform energy into organic compounds. Depending on their energy source, these organisms are classified as photoautotrophs, using ER for photosynthesis (i.e. most plants, green, red and brown algae, cyanobacteria and some bacteria) or chemoautotrophs, using energy released from inorganic chemical reactions (i.e. bacteria and archaea including methanogens, halophiles, sulphur oxidizers and reducers, nitrifiers and thermoacidophiles.). The vast majority of the Earth's primary production results from photosynthesis of plants using ER from the sun, making solar radiation the driving force behind the functioning of nearly all ecosystems (Leuschner 2005). Plants are not only the main producers of biomass and thus central for global energy flow and biogeochemical cycles, they also define the spatial structure in ecosystems and thus habitat availability (Leuschner 2005). Imaging spectroscopy of vegetation has gained considerable importance in ecosystem ecology (Kerr & Ostrovsky 2003; Ustin *et al.* 2004; Aplin 2005), given the growing knowledge on how ecosystem components are linked with each other, the increasing availability of global data sets and the need for global ecosystem assessment, monitoring, protection and restoration schemes (MEA 2005).

1.3 Vegetation maps

In principle, two general types of vegetation maps can be distinguished, maps of potential vegetation and maps of actual vegetation or land cover. The concept of potential vegetation is associated with plant sociology, developed by J. Braun-Blanquet (Braun-Blanquet 1928). On the local scale, relevé data (full floristic inventories) are used to identify the most dominant species combinations determining plant sociological groups, which follow a hierarchical system of Latinate names similar to the taxonomic system of Linné (Schütz *et al.* 2013). For example, when *Sesleria caerulea* L. and *Carex sempervirens* Vill. are dominant in grasslands the plant sociological group is named *Seslerio-Caricetum sempervirentis*. If relationships between plant sociological groups and landscape characteristics, such as topography or soil are known and data on these abiotic characteristics are available, plant sociological groups can be extrapolated within ecologically similar regions (e.g. Fig. 1.5, left). On the global scale, plant sociological groups are often neither conceptually defined nor detectable using remote sensing data. For global mapping approaches, pheno-physiognomic vegetation units defined by structural and seasonal activity patterns, provide an alternative to plant sociological types. Since potential vegetation follows globally detectable ecological processes, such as thermal (energy,

temperature and evaporation fluxes), moisture input, evapotranspiration and accumulation patterns (e.g. carbon storage), environmental envelopes can be combined with pheno-physiognomic vegetation units to assess potential vegetation on the global scale (van der Maarel 2005). The geographic distribution of 50 potential dominant vegetation (PDV) types, such as tropical montane rain forest or Mediterranean conifer forest, was already predicted globally using environmental envelopes (van der Maarel 2005).

In contrast, actual vegetation patterns are routinely predicted and mapped using remote sensing data from the local to the global scale. On the local scale, actual vegetation patterns are assessed using aerial images and are delineated either visually by interpreters or automatically by classification algorithms (e.g. Fig. 1.5, right). On the global scale, the most easily recognizable vegetation units, called vegetation formations, correspond to the world's major ecosystems and are composed of plants with relatively uniform physiognomy but species from the regional floras (Box & Fujiwara 2005). These vegetation formations can already be distinguished using low resolution satellite data (Pfeifer *et al.* 2012; Congalton *et al.* 2014), with the most recent products 'Global Land Cover 2000' (Bartholomé & Belward 2005) and 'MODIS global land cover' (Bicheron *et al.* 2008) being based on MODIS (moderate resolution imaging spectroradiometer) satellite data.

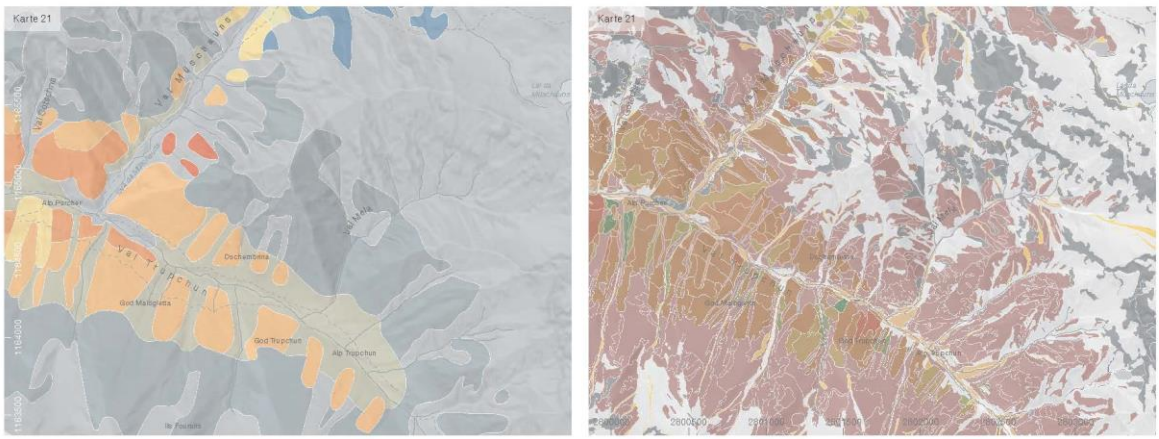


Figure 1.5 Vegetation maps of the Trupchun Valley, Swiss National Park. Map of plant sociological types, based on field surveys from the 1970´s representing the potential vegetation (left) and habitat map, based on aerial image interpretation from the 2000´s, following the NATURA 2000 classification code, representing actual vegetation (right; from Schütz *et al.* 2013).

For assessing and monitoring the state of the Earth's ecosystem both, maps of potential vegetation, indicating ecosystem capacity, and actual vegetation, indicating disturbances and stresses are needed. Additionally, more detailed maps of the distribution of species, functional types and genotypes, as well as vegetation nutrient, water and structural component composition would enable greater realism for ecosystem service assessment. Initiated by the Millennium Ecosystem Assessment (MEA 2005), the research interest in improving existing global vegetation maps has increased. The expected launches of spaceborne instruments, such as Sentinel-2 (planned for 11 June 2015; Drusch *et al.* 2012), EnMAP (planned in 2017, Kaufmann *et al.* 2013), PRISMA (planned in 2017, Lopinto & Ananasso 2013), and HyspIRI (expected after 2022, NASA 2012) with spatial resolutions between 10-20 m (Sentinel-2), 30 m (EnMAP, PRISMA) and 60 m (PRISMA, HyspIRI), will provide the opportunities for refined and consistent large scale vegetation mapping initiatives.

1.4 Research context

The field work for this thesis was carried out in the Swiss National Park (SNP) in the Grisons. Founded in 1914, the SNP is the oldest national park in Central Europe and the country's only national park. As an IUCN (International Union for the Conservation of Nature) category 1a protected area (strict nature reserve), the SNP represents a unique area where nature has been left to itself for over a century. With its foundation, research was set as the SNP´s main objective, with the aim to observe nature at work in an 'outdoor laboratory', undisturbed by human interference (Kupper 2009). Vegetation ecology research has an exceptionally long tradition in the SNP. The first long term observation plots were established by J. Braun-Blanquet in 1917 and have been monitored on a regular basis since. Thanks to its long research tradition building up an extensive database and its strict regulations (e.g. visitors are not allowed to leave the marked paths, no dogs are allowed in the park, the park is closed during winter), the SNP offers an ideal place to study ecosystem processes and to gain a better understanding of how natural areas function. To make the data collected better accessible, a large quantity of spatial datasets and many publications, including historic maps, were digitized (see e.g. Haller *et al.* 2013) and included in the SNP Data Centre (Swiss National Park 2015). However, depending on the research question the vegetation data collected so far had two major shortcomings. They are either very detailed, but representing point data with limited extrapolation possibilities (e.g. relevé data in long term monitoring plots, which can get compiled to define plant sociological types), or they are continuously covering larger areas (extent of the SNP or more), but are based on aerial image interpretation and thus representing only few vegetation classes with coarse spatial resolution (Fig. 1.5).

Many of today's ecological questions, including biodiversity assessment, vegetation change detection, animal movement patterns or nutrient cycling would profit from continuous vegetation data collected at high spatial resolution. One example is ungulate research, defined by the SNP´s directorate as a priority internal research focus in 1996, aiming to investigate the habitat use and movement patterns of the SNP´s three sympatric ungulate species, chamois (*Rupicapra rupicapra* L.), ibex (*Capra ibex* L.) and red deer (*Cervus elaphus* L.). In the following years, several individuals of all three species were equipped with global positioning system (GPS) collars. The spatial distribution of the species was found to differ significantly, but the reason for this was not clear (Haller 2006). Subsequent studies on the species diet composition found no differences in forage composition in spring and summer (Trutmann 2009; Anderwald *et al.* 2013) indicating potential for inter-specific competition. However, these studies were based on micro-histological analyses of faecal pellets identifying plant fragments to the level of growth forms (herbs, grasses, woody plants) or sometimes plant families. As alpine plants can differ significantly in their growth form and nutrient content depending on small scale heterogeneity of micro-climate and soil (Duparc *et al.* 2013), forage classifications at this level might considerably conceal vegetation heterogeneity (Blix *et al.* 2014). Indeed, the animals can be expected to partition their forage resources not on the level of plant families or functional types but rather on the amount of forage available and its nutrient content, which is likely also reflected in their habitat choices. Thus, information on vegetation quantity and quality is needed to tackle the classical question of how ecologically similar species share a common environment.

For the SNP, large ungulates serve as research focal points, but this is not intended to hide the fact that vegetation composition and structure is key to the functioning of the entire grassland ecosystems. The complexity of processes influencing alpine grasslands and the interactions between these processes and the organism community have been studied intensively in the SNP during the last years, including studies on the soil microbial community (Hodel *et al.* 2014; Vandegehuchte *et al.*

2015), herbivores of various body sizes (Schütz *et al.* 2003; Spalinger *et al.* 2012) and ecosystem services, such as nutrient (Schütz *et al.* 2006; Haynes *et al.* 2014) and carbon cycling (Risch *et al.* 2008; Risch *et al.* 2013). Detailed maps of structural and biochemical vegetation characteristics and vegetation composition would allow bringing these ecosystem orientated research activities to the landscape scale.

1.5 Research Questions

The goal of this thesis was to use imaging spectroscopy data collected by the airborne imaging spectrometer APEX during the summers of four consecutive years (2010-2013) and vegetation data from up to 100 research plots to model, predict and map various vegetation characteristics in the alpine grasslands of the SNP. The products developed shall serve as baseline data in different research fields, from vegetation to animal ecology, from ecosystem research to landscape change detection. To elaborate on the applicability of the resulting map products, additional vegetation data from long term vegetation monitoring plots and GPS data of chamois, ibex and red deer were included in the analyses to answer the following research questions:

RQ 1: Can imaging spectroscopy data be used to model plant biomass in highly heterogeneous alpine grasslands?

RQ 2: How much accuracy is lost when extrapolating imaging spectroscopy models of plant biomass to different study areas and different spatial scales?

RQ 3: Can plant functional types (PFTs) be modelled and predicted in heterogeneous alpine grassland and how are PFTs related to spectral response?

RQ 4: Can spectroscopic methods be used to model vegetation quality in heterogeneous alpine grasslands?

RQ 5: Are the movement patterns of three sympatric large ungulate species related to vegetation quantity and quality when mapped at high spatial resolution?

1.6 Structure of the thesis

Chapter 1 gives a brief background and presents the goal, main research questions and structure of this thesis. Chapter 2 describes plant biomass modelling, predicting and mapping with imaging spectroscopy data in the highly heterogeneous grasslands of the SNP and investigates if models can be extrapolated to different study areas and spatial scales within the SNP (RQ 1, RQ 2). Chapter 3 introduces a framework for linking PFTs to structural and biochemical vegetation characteristics and shows how a variety of PFTs can be modelled, predicted and mapped using imaging spectroscopy data in the SNP´s grasslands (RQ 3). Chapter 4 presents the modelling, predicting and mapping of vegetation quality (plant nitrogen content) in the SNP´s grasslands and links the movement patterns of chamois, ibex and red deer to maps of vegetation quantity and quality, explaining how resources can be partitioned in this animal guild (RQ 4, RQ 5). Chapter 5 summarizes and discusses the main findings, provides an outlook on ongoing research activities and possible directions for future research.

2 USING IMAGING SPECTROSCOPY TO PREDICT ABOVE-GROUND PLANT BIOMASS IN ALPINE GRASSLANDS GRAZED BY LARGE UNGULATES

This chapter is modified from: Schweiger A.K., Risch A.C., Damm A., Kneubühler M., Haller R., Schaepman M.E. & Schütz M. (2015). Using imaging spectroscopy to predict above-ground plant biomass in alpine grasslands grazed by large ungulates. Journal of Vegetation Science, 26, 175-190.

Authors' contributions: AKS participated in designing the study, planned and carried out field work, performed the statistical analysis, drafted the initial version of the manuscript, coordinated manuscript preparation and wrote the manuscript. ACR designed the study, planned and carried out field work, provided statistical support and wrote the manuscript. AD supported data analysis and wrote the manuscript. MK designed the study, pre-processed IS data and wrote the manuscript. RH designed the study and wrote the manuscript. MES designed the study and wrote the manuscript. MS designed the study, planned and carried out field work, provided statistical support and wrote the manuscript. All authors read and approved the final manuscript.

Abstract

Imaging spectroscopy enables measuring vegetation optical properties to predict vegetation characteristics that are important for a wide range of ecological applications. Our aim was to predict fresh aboveground biomass of heterogeneous alpine grasslands in two areas and at two ecological scales. Furthermore, we assessed model plausibility for an intensively studied alpine grassland site (plant community scale) featuring distinct biomass and ungulate grazing patterns.

Biomass data were collected in 51 plots and combined with imaging spectroscopy data to establish simple ratio models. We analysed the predictive power and transferability of models developed in two areas (Val Trupchun, Il Fuorn) and at two ecological scales (regional, local). In a next step, we compared our results to the broadband normalised difference vegetation index (NDVI). Finally, we assessed the correlations between model predictions and plant biomass distribution at the plant community scale.

The best local simple ratio models yielded a model fit of $R^2 = 0.60$ and $R^2 = 0.30$, respectively, the best regional model a fit of $R^2 = 0.44$. NDVI model performance was weaker for the regional and one local area, but slightly better for the other local area. However, at the plant community scale only the local model showed a significant positive correlation ($R_S = 0.39$) with the known biomass distribution. Further, predictive power decreased when models were transferred from one local area to another or from one ecological scale to another.

Our study demonstrated that imaging spectroscopy is generally useful to predict aboveground plant biomass in alpine grasslands with distinct grazing patterns. Site-specific local models based on simple ratio indices performed better than the NDVI or regional models suggesting that standardised approaches might not be adequate, particularly in heterogeneous grasslands inhabited by large ungulates. We emphasise the importance of collecting ground reference data covering the expected range of productivity and plant species composition. Moreover, plant community scale data from a previous study proved to be extremely valuable to test model plausibility.

Introduction

Grasslands are spatially and temporally heterogeneous landscape elements. The variability of topo-edaphic parameters creates spatial heterogeneity in soil (texture, moisture, nutrients; e.g. Frank *et al.* 1994; Turner *et al.* 1997) and plant properties (community composition, biomass; e.g. Lauenroth & Sala 1992; Knapp *et al.* 1993). Temporal heterogeneity in soil and plant properties is, in turn, largely related to seasonal and interannual variation in temperature and precipitation regimes (e.g. Lauenroth & Sala 1992; Epstein *et al.* 2002; Knapp *et al.* 2002). Besides these abiotic controls of spatio-temporal variability, herbivores can act as biotic drivers of grassland properties as they have strong direct and indirect effects on ecosystem processes such as nutrient cycling or productivity (e.g. McNaughton 1979; McNaughton *et al.* 1997; Wardle *et al.* 2004; Risch & Frank 2006; De Knegt *et al.* 2008; De Jager & Pastor 2009). Thus, grassland ecosystems are particularly interesting for assessing interactions between environmental parameters, their impact on the heterogeneity and spatio-temporal variability of the vegetation and related activity of the herbivore community.

The spatio-temporal variability in the distribution of forage, i.e., nutritious quality or quantity of plant material, is important for understanding the behaviour of herbivores, since their activities are linked to specific spatial and temporal scales (Skidmore *et al.* 2010). Large ungulates show migration patterns and home range establishment at the regional or landscape scale, they choose suitable feeding areas and plant communities at the local scale and select certain plant species or plant parts at the plant community scale (Senft *et al.* 1987). Consequently, predicting how vegetation quality and quantity varies in space and time is critical for understanding ungulate behaviour and is essential for wildlife conservation (Bailey *et al.* 1996; Ritchie & Olff 1999; Hebblewhite & Haydon 2010). As the amount and quality of vegetation in particular and ecosystem processes in general are, in turn, affected by herbivores, also plant-herbivore interactions change across both temporal and spatial scales (Bestelmeyer *et al.* 2011; Tanentzap & Coomes 2012; Zheng *et al.* 2012). Thus, spatially continuous information on vegetation characteristics at reasonable resolution covering large areas would be advantageous for comprehensively analysing plant-herbivore interactions, since different properties of ecological phenomena emerge when viewed at different scales (Skidmore & Ferwerda 2008).

In situ measurements of spatio-temporally heterogeneous grassland properties take considerable time and effort (Aplin 2005; Milton *et al.* 2009) and often conflict with the need to cover large areas (Ustin *et al.* 2004). Especially in mountainous regions, where the terrain is difficult to access, systematic in situ sampling of vegetation traits within traditional field campaigns is highly laborious. If informative priors, e.g. considering physical factors such as soil properties, or radiation are readily available, extrapolations of vegetation traits from research plots to local scale may sometimes be possible. However, the extrapolation of findings from research plots usually suffers from uncertainties and knowledge gaps. Air- and spaceborne remote sensing provide the only realistic mean to fill these gaps by collecting spatially continuous information on environmental parameters over large areas (Kerr & Ostrovsky 2003; Aplin 2005).

In contrast to broadband sensors, such as Landsat with only a few spectral bands [four (Landsat 1-5) to eight bands (Landsat 8)], fine spatial resolution imaging spectroscopy (IS) offers the advantage of increased spectral sampling using 'hundreds' of spectral bands (Goetz *et al.* 1985). Thus, IS makes it possible to detect the radiometric response resulting from subtle changes in the composition of different land cover types, typically soil or vegetation classes (Ustin *et al.* 2004; Aplin 2005; Wang *et al.* 2010). IS was successfully used to discriminate between plant functional types (e.g. Ustin & Gamon 2010; Schmidtlein *et al.* 2012), individual plant species (e.g. He *et al.* 2011), plant biochemical compositions (e.g. Skidmore *et al.* 2010; Youngentob *et al.* 2012) or available plant biomass (e.g. Mirik

et al. 2005; Numata *et al.* 2008; Cho & Skidmore 2009) and thus has proven highly valuable for several fields of ecosystem research (Ustin *et al.* 2004; Goetz 2009; Schaepman *et al.* 2009).

The radiometric response (i.e. the reflectance spectrum) of vegetation is determined by absorption and scattering of light, which is caused by chemical bonds and the three-dimensional structure of the plant and the canopy (Ustin *et al.* 2004). Specific regions of the spectrum known to be sensitive to these different biochemical or biophysical plant properties (see e.g. Curran 1989) can be combined to calculate spectral indices (SI's; Oldeland *et al.* 2010). For biomass estimation, numerous SI's have been developed during the past decades (for detailed descriptions and discussion of their properties see e.g. Broge & Leblanc 2001; Haboudane *et al.* 2004; Zarco-Tejada *et al.* 2005), with the most commonly used being the normalised difference vegetation index (NDVI; Rouse *et al.* 1974). SI's can be calculated using coarse (broadband) and fine (narrowband; i.e. IS data) spectral resolution data. Broadband SI's, such as the broadband NDVI, are regularly used for comparing vegetation characteristics over large areas (e.g. on the global scale using satellite data) with constrained spatial detail. If information on vegetation characteristics is desired in complex landscapes (with variable percentages of vegetation cover, litter, woody elements and soil etc.) and high spatial detail, narrowband SI's usually provide better results (Asner *et al.* 2000; Thenkabail *et al.* 2002). In combination with ground reference data narrowband SI's allow developing predictive models for vegetation characteristics specifically adapted to a study area. Although the importance of systematic ground sampling during satellite or aircraft overflights was recognised already decades ago (see e.g. Gamon *et al.* 1993), the lack of sufficient and high quality ground reference plots (i.e. covering the expected variability) still often constrains the development of robust models and the implementation of validation and accuracy assessment (Lu 2006).

Generally, the relationship between grassland biomass and spectral indices holds best for moderate to short canopies that contain a high proportion of green, photosynthetically active material (Tucker 1979; Hill 2004). Estimating biomass in more complex, heterogeneous systems is much more challenging (Sims & Gamon 2002; Lu 2006; Cho & Skidmore 2009). Studies using satellite data investigated possibilities of spatial interpolation for predicting biomass (canopy to local scale; Numata *et al.* 2008), measuring the impact of herbivore grazing intensity (Todd *et al.* 1998; Numata *et al.* 2007) and assessing the influence of different plant species and canopy architecture on biomass prediction (Numata *et al.* 2008), but they were carried out in managed rangelands with 1 - 2 dominant grass species. Similarly, airborne IS has already been applied to predict variability in biomass patterns in arable land (e.g. Thenkabail *et al.* 2000; Hansen & Schjoerring 2003; Liu *et al.* 2010) or relatively uniform grassland (Gamon *et al.* 1993). Comparatively few studies have used airborne IS to predict biomass in semi-natural grasslands (e.g. Mirik *et al.* 2005; Beeri *et al.* 2007; Cho *et al.* 2007; Cho & Skidmore 2009) and none of these studies tried to assess both plant biomass and the effects of plant-herbivore interactions within the same heterogeneous grassland ecosystem.

The goal of our study is to use airborne IS data to model vegetation quantity [total aboveground plant biomass (fresh weight; $g.m^{-2}$)] in a highly heterogeneous alpine landscape, where three large ungulate species red deer (*Cervus elaphus* L.), chamois (*Rupicapra rupicapra* L.) and ibex (*Capra ibex* L.) are ubiquitous and therefore strongly interact with the vegetation. More specifically, we used airborne IS data from the Airborne Prism Experiment (APEX; Jehle *et al.* 2010) and ground reference data to develop models for the prediction of biomass in alpine grasslands in two study areas [Val Trupchun (TRU) and Il Fuorn (FUO)] in the Swiss National Park (SNP). We analysed models developed at different ecological scales, i.e. the regional scale (entire SNP, approximately 170 km^2) and the local scale (TRU and FUO, approximately 22 km^2 and 30 km^2, respectively) and tested model transferability i) between the regional and the local scale and ii) between the two local scales. Further, we compared our results

with a more standardised approach, the broadband NDVI. In addition, we tested our models on a small grassland site (Alp Stabelchod, plant community scale, approximately 11 ha) where additional field data for biomass were available (see Schütz *et al.* 2006; Thiel-Egenter *et al.* 2007). It must be noted that the concept of scale can be viewed from a cartographic or an ecological perspective (Skidmore & Ferwerda 2008). While small scale in cartography means to cover a large area in less detail (e.g. global maps of 1:1 000 000), small scale in ecology means to cover a small area in great detail. We relate 'scale' to the conceptual model of large herbivore foraging hierarchy where scales are defined by the frequencies of switches within and between foraging patterns and the boundaries between scale units reflect the animals' behaviour (Senft *et al.* 1987). In the SNP, some individuals of the three ungulate species switch between regional scales during the course of their lifetimes, whereas practically all individuals change at the local scale several times per year. In contrast, the ungulates cross plant community boundaries usually several times per day. Since the three scales of our study (regional, local and plant community scale) relate to the way large ungulates interact with their environment, they are considered as ecologically meaningful subdivisions of the landscape continuum.

The results of this study, i.e. the assessment of a remote sensing based approach to derive spatially continuous information on biomass in a complex alpine environment, will be used to facilitate the analysis of plant-herbivore interactions, which is one of the research priorities in the SNP (see Schütz *et al.* 2003; Risch *et al.* 2004; Suter *et al.* 2004; Schütz *et al.* 2006; Thiel-Egenter *et al.* 2007; Risch *et al.* 2008; Spalinger *et al.* 2012; Risch *et al.* 2013).

Methods

Study area

The study was conducted in the SNP, located in south-eastern Switzerland. Elevation ranges from 1350 m to 3170 m above mean sea level (AMSL). The SNP encompasses an area of approximately 170 km². About 86 km² are covered by vegetation, with forests occupying 53 km² and grasslands 29 km². The average annual temperature is 0.9 ± 0.5 °C (mean ± SD), with a mean annual minimum of -18.8 ± 8.6 °C and a mean annual maximum of 13.6 ± 6.1 °C; mean annual precipitation is 744 ± 160 mm, with an annual minimum of 667 mm and an annual maximum of 1013 mm; mean daily wind speed is 5.3 ± 2.2 km/h with hourly maxima of up to 29.2 km/h and peak gusts of up to 100.8 km/h (2008 - 2012, recorded at the park's weather station Buffalora at 1977 m AMSL; MeteoSwiss 2013). The grasslands in the SNP are characterized by a heterogeneous mosaic-like structure caused by small scale microrelief variability resulting in variations in microclimate and soil properties. The heterogeneity is also reflected in high small scale plant species richness: up to 40 plant species per m² are found. The plant growing season lasts from mid-May until mid-September. The SNP is known for its large populations of red deer, chamois and ibex, with densities of 9.6 red deer, 7.7 chamois and 1.7 ibex per km^2 (2010 population counts).

We selected two study areas within the SNP (regional scale) for developing local biomass models: TRU and FUO (Fig. 2.1). TRU is a south-east to north-west orientated valley that encompasses approximately 22 km^2. About 26% of the area is covered by grasslands; bedrock consists of mainly limestone and calcareous schist. FUO extends over approximately 30 km^2 and consists of several side valleys. About 20% of the area is covered by grasslands and the bedrock is mainly dolomite. Additionally, we used previously published biomass data from Alp Stabelchod (plant community scale), a grassland site of about 11 ha surrounded by forest and located in study area FUO (Fig. 2.1).

Vegetation and soil properties as well as the impact of large ungulates on Alp Stabelchod have been studied intensively on a grid covering the entire site with cells measuring 20 x 20 m (Schütz *et al.* 2003; Schütz *et al.* 2006; Thiel-Egenter *et al.* 2007).

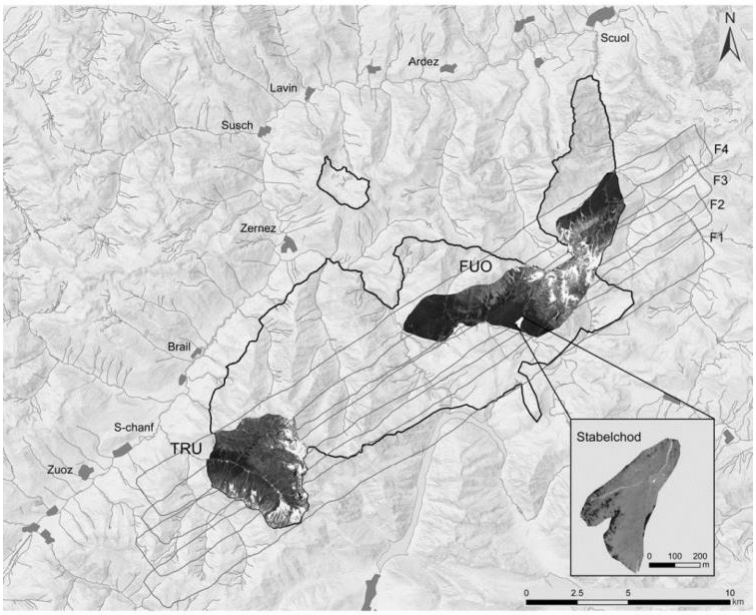


Figure 2.1 Study areas Trupchun (TRU) and Il Fuorn (FUO) located within the Swiss National Park (SNP). Four APEX flight strips (F1, F2, F3, F4) were included in our study. The enlargement in the lower right corner shows Alp Stabelchod.

Ground reference data: Regional and local scale

We established a total of 51 ground reference plots covering the entire range of exposures and elevations and the expected range of grassland biomass, plant species composition and grazing intensity. 25 plots were located in TRU, 26 in FUO (Fig. 2.2). We defined a minimum of 50 x 50 m of grassland area for a ground reference plot to be established and a minimum distance of 20 m between two plots. An individual plot was homogenous in species composition and cover and measured 6 x 6 m to balance possible imprecision resulting from data processing. Plots did not contain large objects (trees, rocks, buildings) or trails and were located at least 6 m from such objects. On June 24, 2010, just after IS data had been acquired (see below), we clipped the vegetation one centimetre above the ground on a 1 x 1 m subplot in the centre of each plot (Fig. 2.2d). The vegetation was immediately sealed into plastic bags and weighed the same day to determine fresh biomass. We then divided the ground reference data into three equally sized groups differing in fresh biomass (low: 20.2 - 250.7 $g.m^{-2}$; medium: 250.7 - 443.3 $g.m^{-2}$; high: 443.3 - 1235.4 $g.m^{-2}$). From each group we randomly assigned half the data to the calibration and half to the validation data set (stratified random sampling).

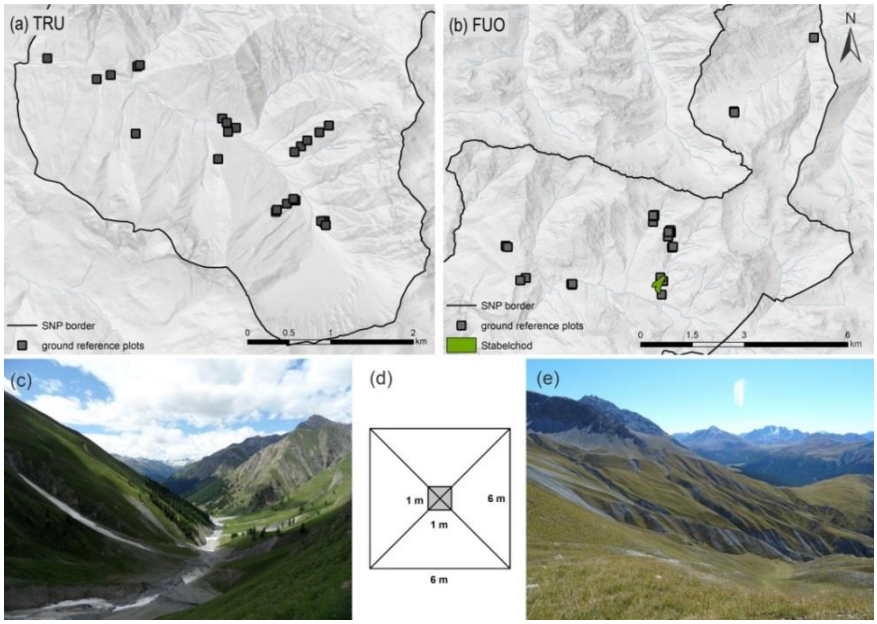


Figure 2.2 Maps and photos of the study areas TRU (a, c) and FUO (b, e), respectively and the design of the ground reference plots (d).

Ground reference data: Plant community scale

Spatially continuous biomass data at the plant community scale are particularly important for the investigation of plant-herbivore interactions. Therefore, we additionally obtained ground reference data for Alp Stabelchod from two previously published data sets to assess model plausibility. One data set contained information on soil phosphorous (soil-P) as well as the proportion of total cover of the two main vegetation types found on Alp Stabelchod (short- and tall-grass vegetation) measured in a 20 x 20 m grid covering the entire grassland (Schütz *et al.* 2006). The second contained grassland aboveground net primary productivity (ANPP g dry weight.m^{-2}) and biomass (g dry weight.m^{-2}) data from an exclosure experiment. The exclosures were located along soil-P gradients in both vegetation types on selected 20 x 20 m grid cells (Schütz *et al.* 2006; Thiel-Egenter *et al.* 2007). In the first step, these data were used to calculate plant biomass for each grid cell. As plant biomass was independent of soil-P regardless of vegetation type (Thiel-Egenter *et al.* 2007), average plant biomass per grid cell was calculated by multiplying the total proportion of short-grass vegetation per grid cell with the average value for short-grass biomass (14.81 g dry weight.m^{-2}) and adding the proportion of tall-grass cover multiplied by the average value for tall-grass biomass (110.9 g dry weight.m^{-2}). In a second step, ANPP and biomass consumption by ungulates was calculated at the same scale. As ANPP was independent of soil-P for short-grass (103.3 g dry weight.m^{-2}), but depended on soil-P in tall-grass vegetation (Thiel-Egenter *et al.* 2007), tall-grass ANPP (ANPP_t) was calculated for each grid cell separately using equation (1).

$$\text{ANPP\_t (g dry weight.m}^{-2}\text{)} = 0.67*\text{soil-P} + 3.29 \quad (1)$$

Average ANPP per grid cell was then calculated using the total proportion of short- and tall-grass cover per grid cell as described for plant biomass. Biomass consumption by ungulates (g dry weight.m^{-2}) was calculated for each grid cell by subtracting plant biomass from ANPP and converted to percent (%).

Imaging spectroscopy data

Imaging spectroscopy data were collected under cloud free conditions on June 24, 2010 between 11.29 and 12.06 central European summer time (CEST) using the airborne imaging spectrometer APEX (Jehle *et al.* 2010). The sun zenith angle was between 31.8° and 28.1°, the sun azimuth between 127.5° and 139.1°, and the mean flight altitude per flight line was between 6665 m and 6667 m AMSL. APEX is a dispersive push broom sensor, mounted on a Dornier DO-228 aircraft operated by Deutsches Zentrum für Luft- und Raumfahrt (DLR, German Aerospace Centre) and covers the wavelength region from 380 nm to 2500 nm in 312 contiguous spectral bands with a full width at half maximum (FWHM) ranging from 4 nm to 12 nm. We used 301 bands for our analysis after removing noisy bands. The spatial sampling interval across track (ground resolution) depends on the flight altitude above ground level (AGL) and is between 1.75 m at 3500 m AGL and 2.5 m at 5230 m AGL. Therefore, the ground pixel size was resampled to 2 x 2 m using a nearest neighbour interpolation (for more details see Schläpfer & Richter 2002). Measured raw digital numbers (DN) of the four flight lines (Fig. 2.1) were converted to radiances by applying calibration coefficients obtained from an after flight calibration campaign (Jehle *et al.* 2010). Calibrated radiance data were then geometrically corrected using a parametric geo-rectification approach implemented in the PARGE software package (Schläpfer & Richter 2002). Surface reflectances, more specifically hemispheric conical reflectance factors (HCRF; see Schaepman-Strub *et al.* (2006), were retrieved from at-sensor radiance data by applying a physically based atmospheric correction approach as implemented in the ATCOR-4 software (Richter & Schläpfer 2002). ATCOR-4 uses the atmospheric radiative transfer model MODTRAN to describe atmospheric absorption and scattering processes and to compensate for their respective impact on the measured at-sensor radiance signals. Parameters describing the atmospheric status required by MODTRAN were set to realistic values (e.g. the CO_2 level was set to 380 ppm) while others like aerosol optical depth or atmospheric water vapour were retrieved pixel-wise from the image data itself. The aerosol size and distribution was approximated with the a-priori defined models 'mid latitudinal summer' and 'rural atmosphere'. Geometric mis-registration of the orthorectified data was evaluated using ground-based differential global positioning system (DGPS) measurements and was found to be less than one pixel (± 2 m) in flat terrain and up to two pixels (± 4 m) on steep slopes (Damm *et al.* 2012). In case that reference plots were covered twice by APEX (overlapping flight lines), both flight lines were used as input for modelling. The two measurements can be considered independent due to reflectance anisotropy effects (caused by differing times of day, flight angles, flight heights, etc.) and are assumed to make our models more robust. Consequently, we had 43 observations for TRU (22 calibration; 21 validation) and 41 observations for FUO (21 calibration; 20 validation).

Model building and mapping

The spectral properties of vegetation are determined by their chemical composition (e.g. pigment concentration, water content), structure (leaf internal and external structure) and the spatial arrangement of these structures (Tucker 1979; Ustin *et al.* 2004; Jones & Vaughan 2010; Wang *et al.* 2010). Three spectral regions are of primary interest for plant biomass assessment (Tucker 1979; Horler *et al.* 1983; Myneni *et al.* 1995; Thenkabail *et al.* 2002): the red (600 - 760 nm), the near-infrared (NIR; 760 - 1100 nm) and the red edge (transition zone between 640 - 760 nm). The more chlorophyll contained in the vegetation the higher the absorption in the red (Tucker 1977; Myneni *et al.* 1995), while a more complex leaf and canopy structure results in more scattering and less absorption in the NIR (Tucker 1979; Curran *et al.* 1991). The red edge is defined as the sharp increase

in the reflectance between these two regions (Horler *et al.* 1983) and thus marks the boundary between chlorophyll absorption and volume scattering (Curran *et al.* 1991; Jones & Vaughan 2010).
Both the calibration plots from TRU and FUO (43 data points) were used to calculate a model valid for the entire SNP (regional model). As the plots measured 6 x 6 m and the pixel size of the IS data was 2 x 2 m, a 3 x 3 pixel aggregation was defined to extract the reflectance measurements from the IS data and to calculate the average reflectance of all 9 aggregated pixels per plot. To test for boundary effects we also calculated the average reflectance over 25 aggregated pixels (5 x 5 pixel aggregations) and found no significant differences between the two (results not shown). This confirms that our ground reference plots were located in homogenous areas on a scale of at least 10 x 10 m. We then calculated all simple ratios (SR = band j/band i) per 9 aggregated pixels per plot for the band combinations located in the spectral regions described above: band j was located in the NIR (760 - 1098 nm; band 76 - 125) and band i in the red part of the spectrum (598 - 756 nm; band 29 - 75), resulting in a total of 2350 combinations. All SRs of the calibration plots were afterwards used as input to model fresh biomass ($g.m^{-2}$) with linear, exponential and second order polynomial functions. Exponential and second order polynomial functions were used to account for potential sources of interference, such as fractions of different vegetation types, surface heterogeneity, or topographic effects. The best model was selected using Akaike´s Information Criterion (AIC) and applied to predict fresh biomass for the entire SNP (both TRU and FUO validation data). Model validation was performed using bootstrapping with 100 replications. We evaluated model fit and predictive accuracy by calculating the coefficient of determination ($R^2 \pm SD$) and the root mean square error (RMSE ± SD). Additionally, we assessed the performance of the regional model (SNP) when used to estimate fresh biomass at the two local scales. Therefore, the best SNP model was validated separately for TRU (using TRU validation data only; thereafter named SNP_TRU) and FUO (using FUO validation data only; SNP_FUO) and model fit and predictive accuracy were calculated.
In a next step, the same method was used to calibrate two local models TRU and FUO separately, using only the TRU and FUO calibration data. The best models were again validated for each study area using the bootstrapping approach and model fit and predictive accuracy were calculated. To assess whether a specific local SR could be used to predict fresh biomass of another local area, the best SR selected for FUO was used to calibrate a model for TRU (using TRU calibration data only; thereafter named FUO_TRU) and the best SR selected for TRU was used to calibrate a model for FUO (using FUO calibration data only; TRU_FUO). Again, the corresponding validation data sets were used for model validation with bootstrapping and model fit and predictive accuracy were calculated. We refer to these models (FUO_TRU and TRU_FUO) as the transferred local models below.
In addition, we simulated broadband NDVI to compare our best regional (SNP) and local models (TRU, FUO) with a more standardised approach. Therefore, we calculated the mean reflectance of all APEX bands in the red (630.5 - 690.0 nm) and NIR (760.4 - 898.1 nm), corresponding to Landsat Thematic Mapper (TM) band 3 and band 4 (i.e., 630 - 690 nm and 760 - 900 nm, respectively) and calculated broadband NDVI (NDVI = NIR – red/NIR + red). Next, we fitted linear models for biomass against the simulated broadband NDVI for the entire SNP and the local areas TRU and FUO, separately using the corresponding calibration data sets. As before, we used bootstrapping to validate the models for each study area and calculated model fit and predictive accuracy.
Finally, we assessed if our regional, local, transferred local and NDVI models succeeded in predicting biomass at the plant community scale (Alp Stabelchod), an intensively studied grassland site with known biomass and consumption rates. Pixel size of the IS data used for the regional and local models was 2 x 2 m, whereas the grid on Alp Stabelchod measured 20 x 20 m. Therefore, the mean predicted biomass was calculated for the 100 2 x 2 m pixels corresponding to each grid cell using the regional

(SNP), local (FUO), transferred local (TRU_FUO) and NDVI model (NDVI_FUO). We calculated the correlation coefficient between biomass at the plant community scale (see method section: 'Ground reference data: Plant community scale') and predicted biomass from our models to assess which of the models best depicted the pattern. For this purpose, either Pearson´s correlation coefficient (R) or Spearman´s rank correlation coefficient (R_S) was used depending on whether the biomass data met the normality and homogeneity criteria.

Since our models were designed to predict only the biomass of grasslands, we applied linear spectral unmixing (LSU) to exclude areas dominated by forest, rock, snow or water from mapping (Roberts *et al.* 1993). Imaging spectroscopy data were prepared using ENVI (version 4.7, Exelis Visual Information Solutions, Boulder, CO, US). For modelling we used R (version 2.15.1, R Development Core Team, Vienna, AT), for spatial data handling and mapping ArcGIS (version 10.0, Environmental Systems Research Institute, Redlands, CA, US).

Results

Fresh weights of aboveground biomass on our 51 ground reference plots ranged from 20.2 g.m^{-2} to 1235.4 g.m^{-2} (354.7 ± 241.7 g.m^{-2}; mean ± SD). For the 25 TRU plots mean biomass was 400.1 ± 265.3 g.m^{-2} (range from 37.2 g.m^{-2} to 1235.4 g.m^{-2}), for the 26 FUO plots mean biomass was 311.1 ± 212.8 g.m^{-2} (range from 20.2 g.m^{-2} to 862.1 g.m^{-2}).

The performance of the best regional model (SNP; Fig. 2.3a) was moderate. However, the broadband NDVI model (NDVI_SNP; Fig. 2.3b) performed considerably weaker, both in terms of R^2 and RMSE.

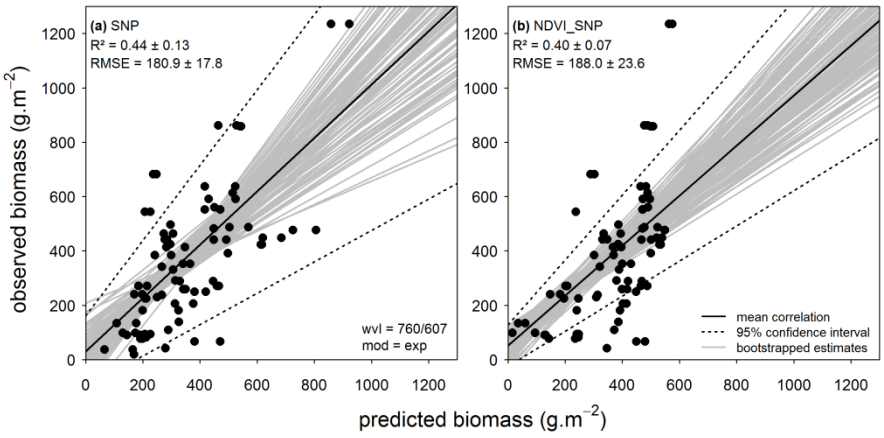


Figure 2.3 Best regional model (SNP; a) and broadband NDVI model (NDVI_SNP; b) predicting fresh biomass at the regional scale. Coefficients of determination (R^2 ± SD), root mean square errors of prediction (RMSE ± SD), wavelengths (wvl) for bands j and i in nm and model type (mod, exp = exponential) are indicated.

In area TRU, the site-specific local model (TRU; Fig. 2.4a) yielded the best fit of all models. The transferred local model (FUO_TRU; Fig. 2.4b), the regional model applied to this local scale (SNP_TRU; Fig. 2.4c) and the broadband NDVI model (NDVI_TRU; Fig. 2.4d) all clearly performed weaker. However, when model predictions were mapped for TRU similar patterns in terms of the high and low biomass became evident (Fig. 2.5). In area FUO, the site-specific local model (FUO; Fig. 2.6a) performed moderately. The transferred local model (TRU_FUO; Fig. 2.6b) performed slightly weaker, the regional model applied to this local scale (SNP_FUO; Fig. 2.6c) and the broadband NDVI model (NDVI_FUO; Fig. 2.6d) performed slightly better, both in terms of R^2 and RMSE.

Most interestingly, only the site-specific local model (FUO) correctly predicted the known biomass pattern on Alp Stabelchod (compare Fig. 2.7a-d with Fig. 2.8a). Previously published data from Alp Stabelchod show high biomass in the western part (Fig. 8a), while high consumption rates of ungulates lead to low biomass in the eastern part of the meadow (Fig. 2.8b). A similar pattern was predicted by the site-specific local model (FUO; Fig. 2.7a), whereas both the regional (SNP_FUO; Fig. 2.7c) and the broadband NDVI model (NDVI_FUO; Fig. 2.7d) predicted the opposite. Predictions of the transferred local model (TRU_FUO; Fig. 2.7b) showed an intermediate prediction featuring no clear differences between the western and eastern parts of the meadow. Correlation analyses revealed that the biomass pattern was, indeed, only correctly reflected by the site-specific local model as we found a positive correlation between measured biomass at the plant community scale and predicted biomass from the model (FUO: RS = 0.39, $p < 0.01$). A negative correlation between measured and predicted biomass was found for the regional (SNP_FUO: R = -0.44, $p < 0.01$) and the broadband NDVI model (NDVI_FUO: RS = -0.43, $p < 0.01$) and a non-significant one for the transferred local model (TRU_FUO: RS = -0.14, $p = 0.10$).

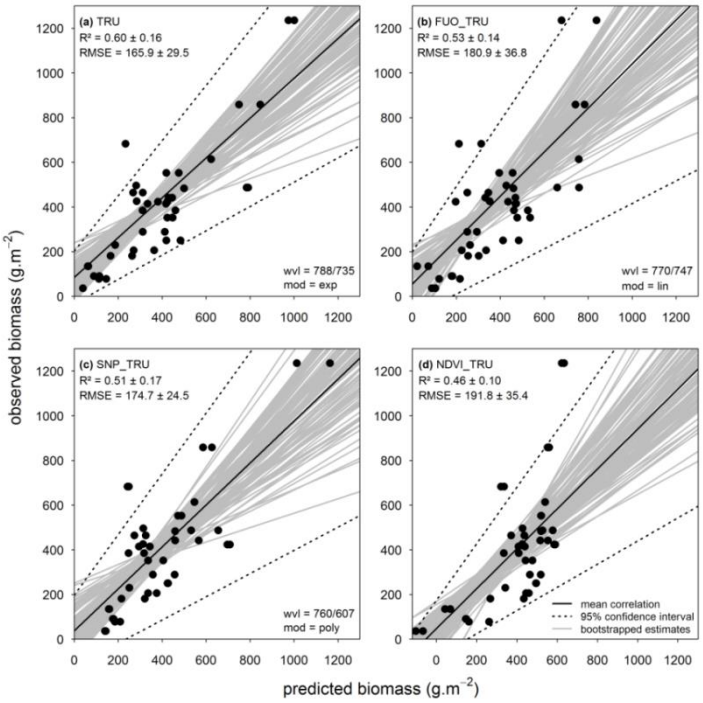


Figure 2.4 Best local model (TRU; a), transferred local (FUO_TRU; b), regional (SNP_TRU; c) and broadband NDVI model (NDVI_TRU; d) predicting fresh biomass at the local scale TRU. Coefficients of determination (R^2 ± SD), root mean square errors of prediction (RMSE ± SD), wavelengths (wvl) for bands j and i in nm and model type (mod, lin= linear, exp = exponential, poly = polynomial) are indicated.

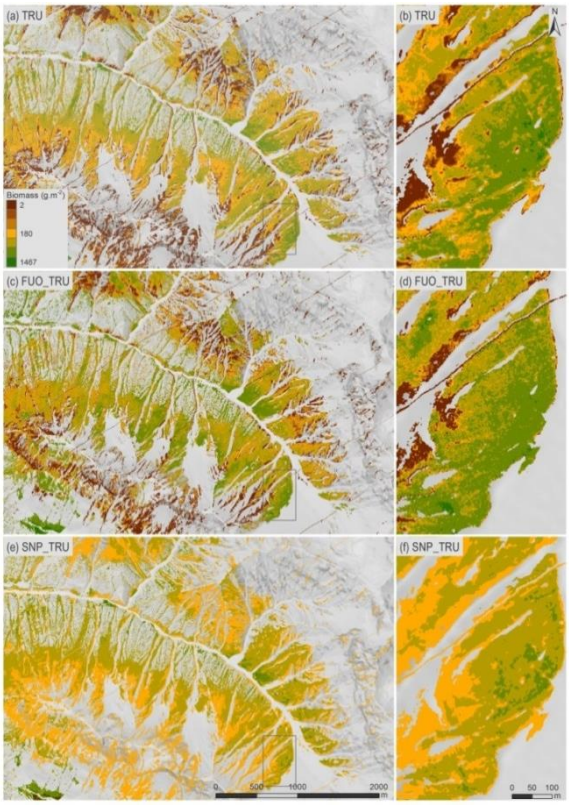


Figure 2.5 Biomass (fresh weight) mapped for TRU using the best local model (TRU; a, b), the transferred local (FUO_TRU; c, d) and the regional model (SNP_TRU; e, f).

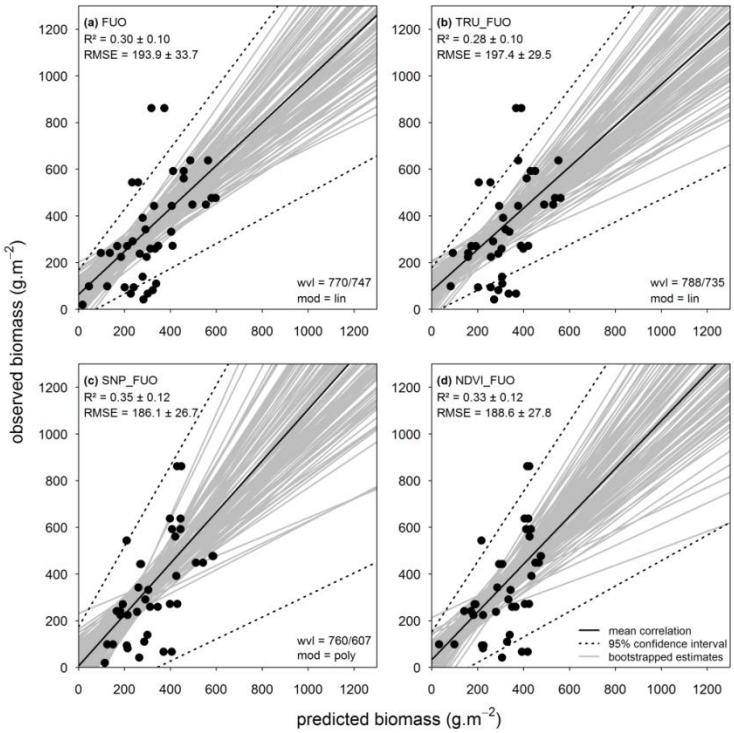


Figure 2.6 Best local model (FUO; a), transferred local (TRU_FUO; b), regional (SNP_FUO; c) and broadband NDVI model (NDVI_FUO; d) predicting fresh biomass at the local scale FUO. Coefficients of determination (R^2 ± SD), root mean square errors of prediction (RMSE ± SD), wavelengths (wvl) for bands j and i in nm and model type (mod, lin= linear, poly = polynomial) are indicated.

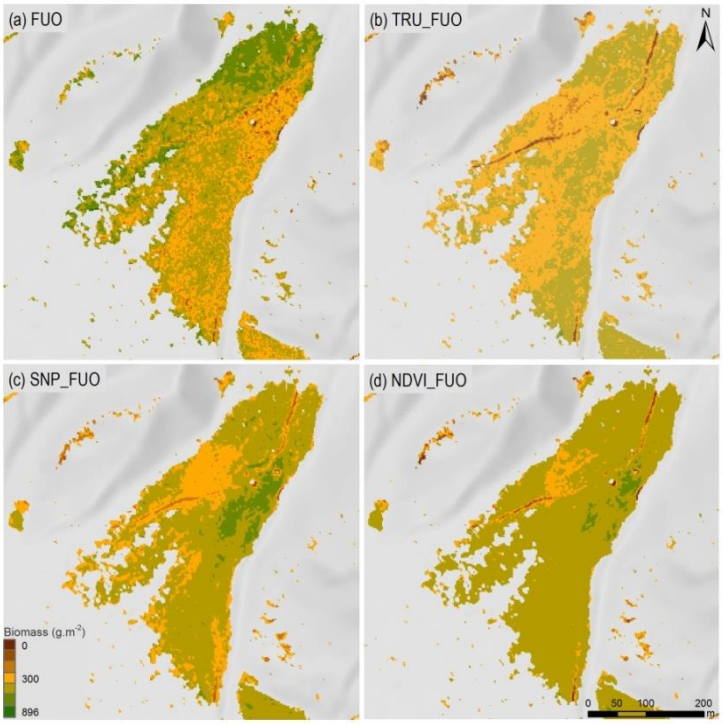


Figure 2.7 Biomass (fresh weight) mapped at the plant community scale (Alp Stabelchod) using the best local model (FUO; a), the transferred local (TRU_FUO; b), the regional (SNP_FUO; c) and the broadband NDVI model (NDVI_FUO; d).

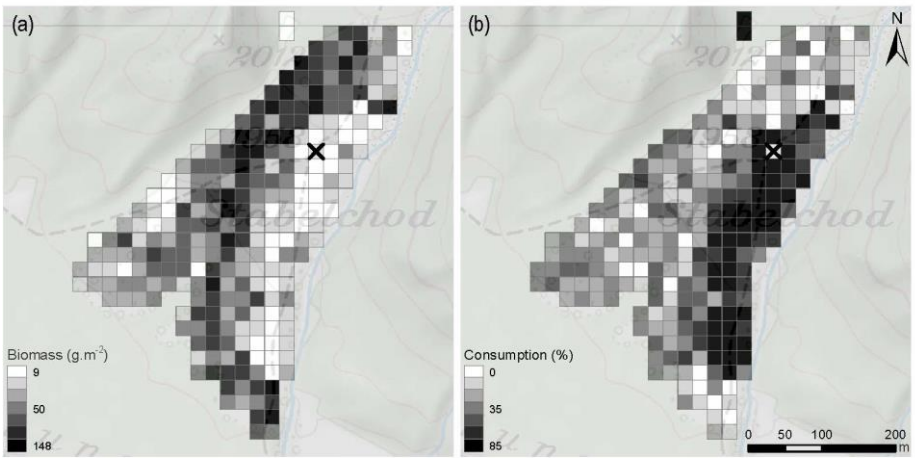


Figure 2.8 Biomass (dry weight; a) and biomass consumption (b) mapped at the plant community scale (Alp Stabelchod) using data from Schütz *et al.* (2006) and Thiel-Egenter *et al.* (2007).

Discussion

Suitability of selected vegetation indices

The simple ratio indices used in this study depended by definition on chlorophyll absorption in the red and volume scattering in the NIR part of the spectrum (Myneni *et al.* 1995; Asner 1998; Jones & Vaughan 2010). Both spectral regions were regularly and successfully used for predicting plant biomass (e.g. Tucker 1979; Mirik *et al.* 2005; Beeri *et al.* 2007; Cho *et al.* 2007; Fava *et al.* 2009). Model fit of the SNP and TRU models (R^2 of 0.44 ± 0.13 and 0.60 ± 0.16, respectively) were in the range of other studies estimating biomass in semi-natural grasslands using airborne IS data. The fit of the FUO model (R^2 of 0.30 ± 0.10) was weaker. Cho *et al.* (2007) and Cho and Skidmore (2009) reported R^2 values of 0.53, 0.56 and 0.64 for biomass estimation in the Italian Apennines, while Beeri *et al.* (2007) and Mirik *et al.* (2005) indicated R^2 values of 0.73 and 0.87 for biomass estimation in the prairies of North Dakota and Wyoming, respectively. The RMSE value of the TRU model (RMSE = 165.9 ± 29.5 $g.m^{-2}$) was only slightly higher than the values between 97.6 $g.m^{-2}$ and 144.7 $g.m^{-2}$ stated by Beeri *et al.* (2007). Again, the predictive accuracy of the FUO model (RMSE = 193.9 ± 33.7 $g.m^{-2}$) was lower. In our opinion, there are several reasons why biomass prediction in study area FUO was more challenging than in TRU. First, the range of biomass values in FUO (20.2 - 862.1 $g.m^{-2}$) was lower than in TRU (37.2 - 1235.4 $g.m^{-2}$). Generally, the trade-off between the range of model parameters and measurement errors leads to model fit becoming weaker when the range of values is comparatively low and measurement errors are high (as it is naturally the case when sampling biomass in the field). Additionally, when classifying slope and aspect based on a 2 x 2 m digital elevation model (DEM) using six classes for slope (< 10 - 20 - 30 - 40 - 50 - > 50%) and eight classes for exposure (N - NO - O - SO - S - SW - W - NW), FUO proved to be more variable than TRU. In study area FUO the four middle classes for slope contained between 11% and 31% of all raster cells and the classes < 10% and > 50% contained each more than 5%, while in area TRU 67% of all raster cells fell in the classes between 30 - 50%. Similarly, all exposure classes in the area FUO contained between 8 - 17% of all raster cells, whereas in area TRU more than 70% of all raster cells were exposed to either N - NO or S - SW. Although topographic variation was minimized by using ATCOR (slope and aspect correction for irradiance at the surface), greater topographic variability in area FUO could have negatively influenced model performance. Moreover, TRU featured a higher proportion of grasslands compared to FUO (26% vs. 20%) and the grassland patches in TRU were larger and less fragmented. Consequently, scattering effects emerging from boundaries between adjacent grasslands and forest or between grassland and rocks (Jiang *et al.* 2012) probably had a greater influence in FUO. Differences in soil reflectance are also assumed to play a role in FUO, where grassland vegetation cover at the small scale was partly less than 100%, while it was almost always 100% or more in TRU. Probably the most important factor influencing model performance in FUO was the high amount of non-photosynthetically active vegetation (NPV) caused by distinct grazing patterns, as we discuss in greater detail below. While Cho *et al.* (2007) and Cho & Skidmore (2009) estimated photosynthetically active vegetation (PV) only and Beeri *et al.* (2007) conducted their study in rangeland where a lower amount of more evenly distributed NPV is expected, up to 50% NPV was found in one vegetation type in area FUO (Schütz, unpublished data).

Interestingly, only the site specific local model FUO correctly reproduced the known biomass pattern at Alp Stabelchod, although both standardised approaches (i.e., the regional SNP_FUO model and the NDVI_FUO model) indicated better model fit. This suggests that standardised approaches might not provide the ideal solution for predicting biomass patterns, particularly in heterogeneous landscapes

with distinct vegetation and grazing patterns. It has been shown that IS is able to detect subtle changes in narrowband absorption features (Ustin *et al.* 2004; Aplin 2005; Wang *et al.* 2010) that are only partially approachable using broadband spectral information (Asner 1998). For example, narrow bands in the red part of the spectrum have proven to be much more sensitive to differences in chlorophyll content (Carter 1998; Jones & Vaughan 2010), a pattern that cannot be fully detected using broad bands (Curran 1994). Additionally, broadband SI's can be unstable, varying with soil colour, canopy structure, leaf optical properties and atmospheric conditions (Huete & Jackson 1988; Middleton 1991; Todd *et al.* 1998). However, site- and sensor-specificity is not only a characteristic of broadband SI's, but of statistical models in general which makes them unsuitable for application in large areas or different seasons/scales (e.g. Curran 1994; Gobron 1997; Cho & Skidmore 2009). Therefore, it was not surprising that our local models performed better than the regional models but were not transferable between sites and scales, as they are highly parameterised for the specific study areas. However, while our models are not transferable, our method – selecting the best site-specific SR index – can also be used in other study areas and seems to be advantageous in heterogeneous grasslands with distinct grazing patterns.

Biomass estimation in a heterogeneous landscape grazed by large ungulates

Biomass estimation using IS data in diverse and heterogeneous communities is challenging (Lu 2006; Cho & Skidmore 2009), since chemical composition and canopy structure is known to vary within and between plant species (Wright *et al.* 2001; Westoby *et al.* 2002). Having, in addition, large ungulates grazing on heterogeneous grasslands makes biomass estimation even more complicated, as ungulates are known to alter plant growth and resource allocation (McNaughton 1979; McNaughton *et al.* 1997; Schütz *et al.* 2006; Risch *et al.* 2007; Frank *et al.* 2011) and therefore the composition and structure of vegetation (Collins *et al.* 1998; Schütz *et al.* 2003; Risch & Frank 2006; Numata *et al.* 2007).

The interaction between ungulate grazing and vegetation community structure can be illustrated for Alp Stabelchod, a grassland site within study area FUO. The vegetation of the eastern part of Alp Stabelchod has been shown to be more nutrient-rich compared to the western one due to differences in former land-use (for more details see Schütz *et al.* 2006). Therefore, large ungulates graze much more intensively (around 60% consumption) on the eastern, compared to the western part of the site (around 16% consumption; cf. Schütz *et al.* 2006). As a consequence of differences in soil nutrient concentrations and grazing intensity, very short (grazed down to 2 cm) but nutrient-rich vegetation containing high levels of chlorophyll predominates the eastern part of Alp Stabelchod. The dominating plant species are grasses, mainly *Festuca rubra* L. and *Briza media* L. and total NPV (senescent grass, litter) is less than 5% (Schütz, unpublished data). On the western part of Alp Stabelchod poorer soils resulted in lower plant quality and therefore lower grazing pressure (higher vegetation; around 20 cm). The dominating plant species is the sedge *Carex sempervirens* Vill. and 30 - 50% of plant material in this vegetation type is NPV (Schütz, unpublished data). Already small amounts of NPV can mask the spectral response in the red part of the spectrum (Roberts *et al.* 1993; Asner 1998; Sellers 1985; Huete & Jackson 1987; Numata *et al.* 2007) and lead to underestimation of biomass in NPV-rich communities (He *et al.* 2006; Beeri *et al.* 2007; Boschetti *et al.* 2007; Verrelst *et al.* 2010). Asner (1998) found that a NPV content of 10% almost doubles, a NPV content of 20% triples and a NPV content of 50% causes a six fold increase in grassland canopy reflectance in the red part of the spectrum. Additionally, since our SR indices depended on the greenness of the vegetation (Tucker 1979; Cohen & Goward 2004), biomass in the chlorophyll rich short-grass might have been overestimated by the regional (SNP_FUO), transferred local (TRU_FUO) and NDVI model (NDVI_FUO). Model improvements

might be achievable when separating NPV from PV and introducing an empirical canopy greenness factor (Gamon *et al.* 1993) or modelling PV only as done in other studies (He *et al.* 2006; Beeri *et al.* 2007; Boschetti *et al.* 2007). However, in our opinion including both, NPV and PV for estimating biomass is important since both contribute to biogeochemical cycling and are essential components of ecosystem functioning (Beeri *et al.* 2007). For grazed systems, Numata *et al.* (2008) suggested sorting NPV from PV after clipping the biomass in the field and combining two separate indices, one for NPV and one for PV. However, this approach would be extremely laborious since single grass leaves are often composed of dead and living parts that would need to be separated. A less time consuming approach would be spectral unmixing to determine the proportion of NPV and PV per pixel (see e.g. Gamon *et al.* 1993; Roberts *et al.* 1993; Asner & Heidebrecht 2002; Numata *et al.* 2007). However, both endmembers, PV and NPV, are producing volume scattering which generates ambiguities in the unmixing process. Thus, a non-linear unmixing approach would be most appropriate here. This would require additional field spectrometer measurements, since the spatial resolution of APEX is too coarse to collect pure pixels from the image when the vegetation is highly heterogeneous and mosaic-like (as in our case). Nevertheless, it would be worth testing this approach in a future study. The differences in vegetation communities and NPV distribution between heavily and lightly grazed areas were expected to be less distinct in TRU, which additionally explains why the TRU models had higher predictive power. As more forage is available in this area (TRU: 400.1 ± 265.3 $g.m^{-2}$ (mean ± SD); FUO: 311.1 ± 212.8 $g.m^{-2}$) grazing is more evenly distributed. Therefore, overall grazing pressure is lower and grazers do not increase vegetation heterogeneity as much as in FUO.

The challenge in applying satellite or aircraft images to ecological studies lies in relating spectral and spatial information in an image to the vegetation pattern and processes on the ground (Gamon *et al.* 1993). Although some improvement through the application of different modelling techniques (e.g. spectral unmixing) might be possible, the fact that the local FUO model correctly predicted the biomass pattern on Alp Stabelchod known from previous studies was thus a success. Recalling the high predictive accuracy of the TRU model, we are confident that our sampling design covered vegetation heterogeneity within both local areas and that our site-specific local models are suited as baseline data for detailed analysis of plant-herbivore interactions.

Conclusions

Our study shows that fine spatial resolution imaging spectroscopy can be successfully used to predict fresh aboveground biomass in a highly heterogeneous alpine landscape with distinct grazing patterns. More specifically, our site-specific local models based on SR indices performed better than regional or NDVI models suggesting that standardised approaches might not always provide the best solution for predicting biomass in challenging landscapes. However, when following our modelling approach two issues should be considered: First, since statistical models are highly site and sensor specific (Curran 1994; Gobron 1997), attention should be given to understanding the applicable scale defined by the characteristics of input data to the original model (Lu 2006). As demonstrated in our study, statistical models developed for one study site should not be transferred to another or used to predict patterns at other scales without checking for plausibility. For this purpose, independent data, ideally sampled on a continuous, relatively fine grid, are highly advantageous. Second, since the availability of sufficient and high-quality ground reference plots often limits the development of robust biomass models and the validation of the results (Lu 2006), a sampling design covering the entire expected range of biomass and heterogeneity should be used. If the distribution of NPV and PV is uneven, separating NPV from PV in the modelling phase should be considered.

3 LINKING PLANT FUNCTIONAL TYPES TO THE SPECTRAL RESPONSE: A TOOL FOR GLOBAL ECOSYSTEM SERVICE ASSESSMENT

This chapter is modified: Schweiger A.K., Schütz M., Risch A.C., Kneubühler M., Haller R. & Schaepman M.E. Linking functional and spectral response of the vegetation community: A tool for global ecosystem service assessment. Submitted to Ecology Letters.

Authors' contributions: AKS participated in designing the study, planned and carried out field work, performed the statistical analysis, drafted the initial version of the manuscript, coordinated manuscript preparation and wrote the manuscript. MS designed the study, planned and carried out field work, provided statistical support and wrote the manuscript. ACR designed the study, planned and carried out field work, provided statistical support and wrote the manuscript. MK designed the study, pre-processed imaging spectroscopy data and wrote the manuscript. RH designed the study and provided comments to the manuscript. MES designed the study and wrote the manuscript. All authors read and approved the final manuscript.

Abstract

The comparability and integrating nature of plant functional types (PFTs) and advances in observational methods such as imaging spectroscopy make their combination highly interesting for assessing ecosystem functions and services. Depending on physical environment and stresses, plants invest in co-varying structural and biochemical traits causally linked to PFTs. The vegetation`s spectral response mirrors these traits, but its connection to PFTs has yet to be established. We test correlations between vegetation traits and PFTs using relevé data from heterogeneous grasslands, introduce a conceptual framework linking the functional and spectral signatures of the vegetation community, and suggest partial least squares regression coefficients as proxies for community level functional trait types. We tested our framework using imaging spectroscopy data and modeled four categories of PFTs (life forms, growth forms, CSR strategy types, indicator values) with high accuracies. External validation confirmed model performances; an encouraging result for using PFTs in large-scale ecosystem services assessment.

Introduction

Improving ecological prediction and forecasting (Petchey *et al.* 2015) to coherently feed properties into assessing ecosystem functions and services is an essential activity supporting conservation of natural resources, sustainable development and human wellbeing, particularly in view of accelerated global change (MEA 2005). While vegetation community composition varies both among and within biomes, the roles and functions of plants in ecosystems remain comparable (Ustin & Gamon 2010). Roles and functions of plants are linked to investment strategies, reflected in structural and biochemical traits (Lavorel *et al.* 1997; Tilman *et al.* 1997), which follow global patterns (Reich *et al.* 1992; Wright *et al.* 2004). As natural selection acts on interacting trait systems (Mayr 1983), plants with a common set of co-varying traits (Zonneveld 1983; Grime *et al.* 1997) can be grouped into plant functional types (PFTs; Lavorel *et al.* 1997; Tilman *et al.* 1997). Within ecosystems plants have to cover different roles and functions, thus plant functional diversity - the value, range and relative abundance

of PFTs within the community (Díaz & Cabido 2001) - is key for delivering ecosystem services (Lavorel 2013).

Observational approaches, such as remote sensing, enable acquiring spatially continuous data over large areas in high spatial, temporal and spectral resolution (Schaepman *et al.* 2009). Thus, information on vegetation traits estimated from remote sensing allow for spatially and temporally consistent ecosystem assessments (Ustin & Gamon 2010; Andrew *et al.* 2014). Moreover, remote sensing enables data acquisition in areas with limited accessibility and - although ground-based data are needed for model validation and interpretation (MEA 2005) - reduces the time and effort involved in field campaigns. As data access increases (Ustin & Gamon 2010), remote sensing promotes global cooperation in developing standardized assessment schemes, utilizing local knowledge while diminishing financial limitations.

The remote sensing community has recognized the potential of using PFTs for assessing ecosystem functions and services (Andrew *et al.* 2014; De Araujo Barbosa *et al.* 2015). However, there is neither agreement on which PFTs to include in ecosystem services assessment, nor on which PFTs are suitable for remote sensing applications (Ustin & Gamon 2010). From an ecological point of view PFTs have to be relevant indicators for specific ecosystem functions and services, while in remote sensing their detectability is of greatest importance (Andrew *et al.* 2014). For ecological questions PFTs have therefore to be selected based on the ecosystem functions and services under study and are preferably used in combination (Kattge *et al.* 2011). When detectability is the main concern, the high spectral dimensionality of imaging spectroscopy data provides the opportunity to predict and map a series of vegetation traits (Schaepman *et al.* 2015), even in highly heterogeneous ecosystems, such as grasslands, where biomass (e.g. Everitt *et al.* 1989; Schweiger *et al.* 2015), plant dry matter (DM; e.g. Vohland & Jarmer 2008), nitrogen (N; e.g. Asner *et al.* 2014) and fiber content (e.g. Starks *et al.* 2004) have already been successfully predicted and mapped.

Generally, the spectral response of vegetation is determined by reflection, transmittance, absorption and scattering of light, caused by chemical bonds and the three-dimensional structure of the plant and the canopy (Curran 1989). While certain regions of the spectrum are known to be sensitive to plant structural or biochemical traits (see e.g. Curran 1989), other traits involve several, partly overlapping spectral regions (Kokaly *et al.* 2009). Detecting structural or biochemical traits in an over-determined spectral response was a common problem in chemometrics (Martens 2001), that can be readily solved using pattern detection techniques, such as partial least squares regression (PLSR; Wold *et al.* 1983). As the independent effects of structural and biochemical traits are largely preserved in the overall shape of the spectral response, pattern detection techniques can also be applied to imaging spectroscopy data (Kokaly *et al.* 2009), an approach called spectroscopic remote sensing. We build upon this spectroscopic approach and suggest that the spectral signature of PFTs is likewise preserved in the vegetation community's spectral response, making it possible to retrieve structural, biochemical and functional vegetation characteristics simultaneously.

The goals of our study were to i) test the correlations between structural and biochemical traits and PFTs on the vegetation community level; ii) provide a conceptual framework for modeling PFTs with imaging spectroscopy data that links the theory, methodology and tools of vegetation ecology and imaging spectroscopy; iii) apply pattern detection techniques (PLSR) to connect the spectral response to PFTs; and iv) use PLSR coefficients to model and predict a series of PFTs at the vegetation community level. More specifically, we tested the correlations between biomass, DM, N and neutral detergent fiber (NDF) content and 14 PFTs of four categories: i) plant life forms; ii) growth forms of graminoids; iii) CSR (competitor (C), stress-tolerator (S), ruderal (R)) strategy types following Grime (1977); and iv) indicator values following Ellenberg *et al.* (1992). These tests formed the basis for our

conceptual framework linking the vegetation's functional to its spectral response. We then used in-situ botanical relevé and airborne imaging spectroscopy data from alpine grasslands to model and predict all PFTs and validated our models with an independent relevé data set (external validation).
We suggest that PLSR coefficients derived from spectroscopic remote can serve as proxies for community level functional trait types (FTT), which link the functional and spectral signatures of the vegetation community to its structural and biochemical traits. This connection enabled us to accurately model and predict a series of characteristically different PFTs in a highly heterogeneous ecosystem. Our results encourage global initiatives joining spectral, PFT and plant trait databases, which hold great potential for future global ecosystem services assessment schemes.

Methods

Study area

Our study area, the Swiss National Park (SNP), is located in southeastern Switzerland (46° 37′ N, 10° 5′ E). The SNP was founded in 1914 and is classified by the IUCN (International Union for the Conservation of Nature) as a category 1a strict nature reserve. About 86 km² of the SNP´s total area (172 km²) are covered by vegetation, with forests occupying 53 km² and grasslands 29 km². Elevation ranges from 1350 to 3170 m a.s.l., average annual precipitation is 754 ± 164 mm (mean ± SD), average annual temperature is 0.9 ± 0.5 °C, with average annual minima of -29.1 ± 2.7 °C and average annual maxima of 24.5 ± 1.0 °C (recorded between 2004 and 2013 at 1968 m). The SNP's grasslands are highly heterogeneous due to large micro-relief variability that influences physical and chemical characteristics of the soil and micro-climatic properties. The plants' growing season lasts from mid-May until mid-September.

Imaging spectroscopy data

Imaging spectroscopy data were collected on June 24, 2010 between 09.01 and 11.50 hours local time using the imaging spectrometer APEX operated on board a Dornier DO-228 aircraft. APEX is a dispersive pushbroom imager covering the wavelength range between 372 to 2540 nm with 312 spectral bands and a spectral sampling width ranging from 0.86 to 12.3 nm (Schaepman et al. 2015). We used 284 bands for analysis after removing noisy bands. The ground sampling distance depends on flight altitude, ranging from 2.50 to 1.75 m (aircraft-ground distance between 5230 and 3500 m). All data were resampled to a regular pixel size of 2 x 2 m using nearest neighbour interpolation (Schläpfer & Richter 2002). Imaging spectroscopy data were geometrically and atmospherically corrected using an atmospheric radiative transfer model (MODTRAN-5) as implemented in PARGE (Schläpfer & Richter 2002) and ATCOR-4 (Richter & Schläpfer 2002). Remaining geometric mis-registration of the orthorectified data were evaluated and found to be less than one pixel (± 2 m) in flat terrain (Damm et al. 2012) and up to two pixels (± 4 m) on steep slopes.

Botanical data

We collected structural and biochemical trait and relevé data in 50 plots measuring 6 x 6 m in the SNP's grasslands (further referred to as research plot data (RPD)). The plots covered a wide range of expositions, altitudes, productivity and vegetation communities, but were placed in areas homogeneous in plant species composition and cover (for details see Schweiger et al. 2015). To assess structural and biochemical vegetation community traits, we clipped one m² of vegetation on the day of the APEX overflight in the centre of each plot. We immediately sealed the samples into plastic bags, determined fresh (g.m-2) and oven-dry biomass (g.m-2; dried at 65°C for 48 h) and calculated DM content (mg.g-1; DM = oven-dry biomass / fresh biomass). Nitrogen (in percent (%)) and NDF content (in %) were chemically analysed using standard laboratory methods (TruSpec CN Analyzer, Leco Corp., St Joseph, MI; Fiber Analyzer 200, Ankom Technology, Macedon, NY) on 24 of our 50 samples. These samples were used to re-calibrate laboratory near-infrared reflectance spectrometer (NIRS) models (NIR Multi-purpose analyser, Bruker Optics, Fällanden, CH), generated from more than 300 vegetation samples collected within the SNP in previous years. Nitrogen and NDF content of all 50 RPD samples were then predicted based on the NIRS models with precisions of $R^2 = 0.93$ (N) and $R^2 = 0.81$ (NDF). For relevé data collection, we estimated plant species cover (in %) in 1 x 1 m quadrates randomly placed within the 50 research plots, but avoiding previously clipped areas. In total 170 plant species were detected in the RPD, ranging from 6 to 41 species per plot.

An independent relevé dataset (further referred to as permanent plot data (PPD)) was obtained from the SNP's long-term permanent grassland monitoring project, which was started in 1917. Briefly, 160 permanent plots of variable size and distributed over the entire area of the SNP are visited every 5 to 10 years and plant species cover (in %) is recorded for all species occurring in the plot. We selected data collected between 2006 and 2014, resulting in PPD from 36 plots, measuring between one and 320 m2 in size and distributed over the entire SNP. Again, the PPD covered a wide range of exposition, altitude, productivity and vegetation communities. In total 224 species were detected in the PPD, ranging from 4 to 81 species per plot.

For allocating life and growth forms we classified each plant species as graminoid, forb, legume or shrub (life form), subdivided the graminoids into tussock and stolon plants (growth form) according to their dominant habitus in the SNP's grasslands and summed their cover % in each plot. For the allocation of CSR strategy types and indicator values (for soil nutrients, soil moisture, light conditions and mowing tolerance) we used Landolt & Bäumler (2010), which list ecological characteristics of 5500 central European plant species. We standardized the RPD and PPD to 100% cover per plot and multiplied both plots x species matrices with the CSR strategy type scores and indicator values matrices, respectively (see Wildi 2010). Species classified as indifferent or with missing indication were omitted.

The resulting plots x PFT matrices (i.e. plots x life forms, plots x growth forms, plots x CSR strategy types and plots x indicator values) were used to calculate Spearman's correlation coefficients (RS) between vegetation community traits (i.e. biomass, DM, N, NDF content) and all PFTs of the four categories. The resulting correlation matrix formed the causal background for developing a conceptual framework linking the functional to the spectral response of the vegetation community by using PLSR coefficients as proxies for community level FTTs.

Modelling

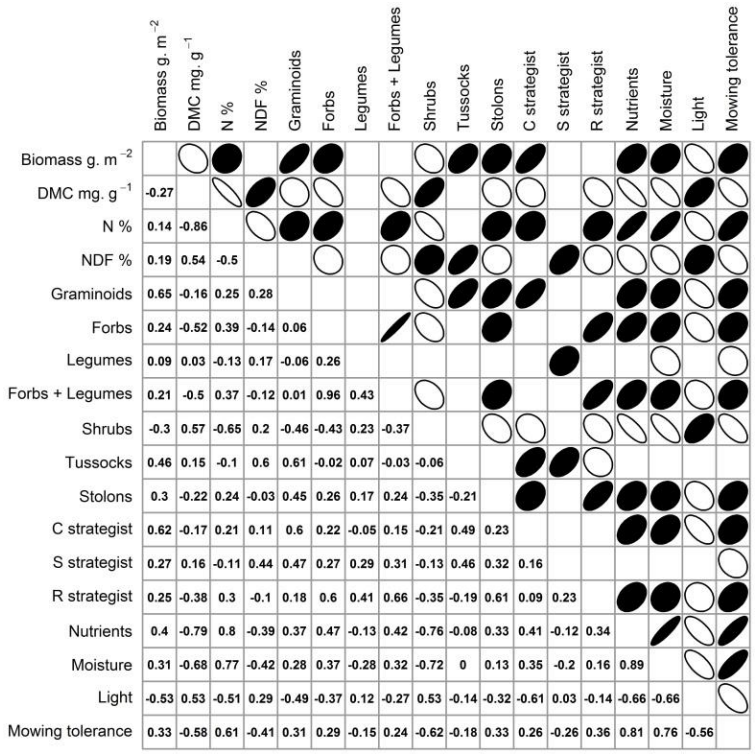
We used PLSR (Wold et al. 1983) implemented in the R pls package (Mevik et al. 2013) to model each PFT using the plots x PFT matrices (functional signature) of the RPD as dependent and the plots x spectral response matrices from APEX data (spectral signature) as predictor variables. Since plots where RPD was collected measured 6 x 6 m and APEX pixel size was 2 x 2 m, we calculated the mean reflectance per plot using a 3 x 3 pixel window (see also Schweiger et al. 2015).

We applied leave-one-out cross-validation and limited the number of PLSR components by minimizing the cross-validated estimate of the root mean squared error of prediction (RMSEP). To evaluate model fit, we determined the correlation coefficient of multiple determination for the cross-validated predictions (R^2) and Theil's uncertainty coefficient (Theil's U), which has the advantage of taking deviations of the slope (from 1) and intercept (from 0; Smith & Rose 1995) into account. Values of Theil's U < 0.2 indicate high and values between 0.2 and 0.4 indicate moderately high predictive power. To compare model performance between the different PFTs we calculated the RMSEP in percentage of the response range (RMSEP %) as well as the proportion of samples predicted within less than 30% mean prediction error (< MPE %).

Finally, we conducted external model validation by comparing the predictions of the best PLSR models with the PFTs determined in the PPD. We extracted the predicted values of all pixels within each PPD plot and calculated the mean predicted value for every PFT per plot. Then, we regressed the mean predicted PFTs against the plots x PFT matrices of the PPD and calculated R^2, Theil's U, RMSEP (%), and the samples predicted within less than 30% MPE (%). We used the image-based software ENVI+IDL (version 4.7, Exelis Visual Information Solutions, Boulder, CO) to extract reflectance values from and apply the PLSR models to the APEX data. All other analyses were conducted in R (version 3.1.2, R Core Team 2014).

Results

Correlation analyses between structural and biochemical vegetation community traits (biomass, DM, N and NDF content) and 14 PFTs of four categories (plant life forms, growth forms of graminoids, CSR strategy types and indicator values) revealed strong significant relationships for many of the pairs tested (Fig. 3.1). These correlations formed the basis for a conceptual framework using PLSR model coefficients as proxies for community level FTTs to link the functional to the spectral signatures of the vegetation community (Fig. 3.2). The resulting PLSR models did perform well regardless of PFT category (Table 3.1, Fig. 3.3). We found good model fit and accuracy for the life forms graminoids, forbs and shrubs, the growth form tussocks, the strategy types C, S and R, and the indicator values for soil nutrients, soil moisture and mowing tolerance (Table 3.1, Fig. 3.3). Legumes (life form), stolons (growth form) and light availability (indicator value) could, in contrast, not be predicted with high accuracy. Yet, when combining forbs and legumes good model fit and accuracy was achieved.



	Biomass g. m⁻²	DMC mg. g⁻¹	N %	NDF %	Graminoids	Forbs	Legumes	Forbs + Legumes	Shrubs	Tussocks	Stolons	C strategist	S strategist	R strategist	Nutrients	Moisture	Light	Mowing tolerance
Biomass g. m⁻²		-0.27	0.14	0.19	0.65	0.24	0.09	0.21	-0.3	0.46	0.3	0.62	0.27	0.25	0.4	0.31	-0.53	0.33
DMC mg. g⁻¹	-0.27		-0.86	0.54	-0.16	-0.52	0.03	-0.5	0.57	0.15	-0.22	-0.17	0.16	-0.38	-0.79	-0.68	0.53	-0.58
N %	0.14	-0.86		-0.5	0.25	0.39	-0.13	0.37	-0.65	-0.1	0.24	0.21	-0.11	0.3	0.8	0.77	-0.51	0.61
NDF %	0.19	0.54	-0.5		0.28	-0.14	0.17	-0.12	0.2	0.6	-0.03	0.11	0.44	-0.1	-0.39	-0.42	0.29	-0.41
Graminoids	0.65	-0.16	0.25	0.28		0.06	-0.06	0.01	-0.46	0.61	0.45	0.6	0.47	0.18	0.37	0.28	-0.49	0.31
Forbs	0.24	-0.52	0.39	-0.14	0.06		0.26	0.96	-0.43	-0.02	0.26	0.22	0.27	0.6	0.47	0.37	-0.37	0.29
Legumes	0.09	0.03	-0.13	0.17	-0.06	0.26		0.43	0.23	0.07	0.17	-0.05	0.29	0.41	-0.13	-0.28	0.12	-0.15
Forbs + Legumes	0.21	-0.5	0.37	-0.12	0.01	0.96	0.43		-0.37	-0.03	0.24	0.15	0.31	0.66	0.42	0.32	-0.27	0.24
Shrubs	-0.3	0.57	-0.65	0.2	-0.46	-0.43	0.23	-0.37		-0.06	-0.35	-0.21	-0.13	-0.35	-0.76	-0.72	0.53	-0.62
Tussocks	0.46	0.15	-0.1	0.6	0.61	-0.02	0.07	-0.03	-0.06		-0.21	0.49	0.46	-0.19	-0.08	0	-0.14	-0.18
Stolons	0.3	-0.22	0.24	-0.03	0.45	0.26	0.17	0.24	-0.35	-0.21		0.23	0.32	0.61	0.33	0.13	-0.32	0.33
C strategist	0.62	-0.17	0.21	0.11	0.6	0.22	-0.05	0.15	-0.21	0.49	0.23		0.16	0.09	0.41	0.35	-0.61	0.26
S strategist	0.27	0.16	-0.11	0.44	0.47	0.27	0.29	0.31	-0.13	0.46	0.32	0.16		0.23	-0.12	-0.2	0.03	-0.26
R strategist	0.25	-0.38	0.3	-0.1	0.18	0.6	0.41	0.66	-0.35	-0.19	0.61	0.09	0.23		0.34	0.16	-0.14	0.36
Nutrients	0.4	-0.79	0.8	-0.39	0.37	0.47	-0.13	0.42	-0.76	-0.08	0.33	0.41	-0.12	0.34		0.89	-0.66	0.81
Moisture	0.31	-0.68	0.77	-0.42	0.28	0.37	-0.28	0.32	-0.72	0	0.13	0.35	-0.2	0.16	0.89		-0.66	0.76
Light	-0.53	0.53	-0.51	0.29	-0.49	-0.37	0.12	-0.27	0.53	-0.14	-0.32	-0.61	0.03	-0.14	-0.66	-0.66		-0.56
Mowing tolerance	0.33	-0.58	0.61	-0.41	0.31	0.29	-0.15	0.24	-0.62	-0.18	0.33	0.26	-0.26	0.36	0.81	0.76	-0.56	

Figure 3.1 Correlation matrix between structural and biochemical vegetation community traits (biomass (Biomass g.m-2), dry matter (DM mg.g-1), nitrogen (N %) and neutral detergent fibre (NDF %) content) and 14 plant functional types of four categories: plant life forms (graminoids, forbs, legumes, forbs + legumes combined, shrubs; cover %), growth forms of graminoids (tussocks and stolons; cover %), CSR strategy types (competitor (C), stress-tolerator (S), ruderal (R); scores), and indicator values (soil nutrients, soil moisture, light, mowing tolerance). The upper triangle shows significant correlations only ($p < 0.05$), the direction (black = positive, white = negative) and strength of the correlation (thick ellipse= weak, thin ellipse = strong). The lower triangle shows the values for Spearman's correlation coefficient (RS).

The external model validation using the PPD supported good model performance for the life forms forbs and shrubs, the strategy types C, S and R, and the indicator values soil nutrients, soil moisture and mowing tolerance. Even though PLSR models based on the RPD did not fit light availability very well, external validation resulted in good model performance for this indicator value. In contrast, while model fit and accuracy for forbs and legumes combined, as well as for tussocks and graminoids (tussocks and stolons) were quite good in the RPD models, they did not hold up in external validation. Unsurprisingly, the PLSR models were not able to predict legumes and stolons in the PPD as the RPD models did not perform well either.

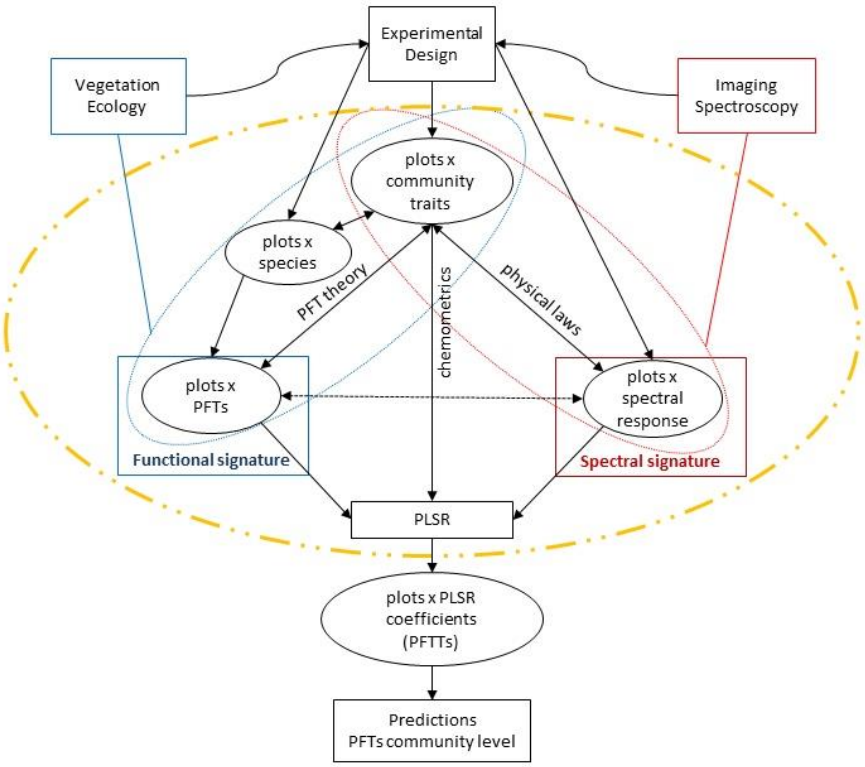


Figure 3.2 Conceptual framework using theory and methodology of vegetation ecology (blue ellipse) and imaging spectroscopy (red ellipse) to link the functional to the spectral signature of the vegetation community. According to plant functional type (PFT) theory, the vegetation community (plots x species) integrates environmental conditions and allocates resources towards the expression of co-varying structural and biochemical traits (plots x community traits), measureable in the field (experimental design) and causally linked to PFTs (plots x PFTs). The reflectance measured with imaging spectroscopy (plots x spectral response) is determined by reflection, transmittance, absorption and scattering of light (physical laws), which again depend on structural and biochemical traits (plots x community traits). In this study (orange ellipse), we connect PFTs and the spectral response via their link to community traits and suggest PLSR model coefficients, commonly used in chemometrics, as proxies for functional traits types (FTTs), to predict PFTs on the community level.

Discussion

The correlation structure (Fig. 3.1) links vegetation community traits and PFTs, which ultimately allows detecting the PFTs in the spectral response. Our results showed that linking PFTs and the spectral response is not only possible, but that the models allow predicting a series of characteristically different PFTs with high accuracy, which was confirmed by external model validation.

For example, the shrubs in our study area are predominantly dwarf shrubs adapted to stressful environments and thus investing relatively little in photosynthesis, mirrored in their strong positive correlation with DM and their strong negative correlation with N content (R_S for DM = 0.57, R_S for N = 0.65; Fig. 3.1). Tussocks protect themselves from herbivores – which considerably influence the SNP's grasslands (e.g. Schütz *et al.* 2006, Risch *et al.* 2013) - through investments in a dense growth form (Coughenour 1985) containing large amounts of litter or unpalatable compounds (e.g. high NDF content), which is reflected in the correlation structure (R_S for biomass = 0.46, R_S for NDF = 0.6; Fig. 3.1). The spectral signatures of these traits is well defined (e.g. Kokaly & Clark 1999), allowing

them to be detectable in the functional signature of the vegetation community. Legumes could not be well predicted with our PLSR models, although we expected them to have a distinct spectral signature through their generally high N content. Most likely, their abundance in the RPD was too low to successfully link their functional and spectral signatures, indicated by the lack of significant correlations between legume cover and vegetation community traits (Fig. 3.1).

Table 3.1 Results of PLSR models using research plot data (RPD) to model 14 plant functional types of four categories and external validations using permanent plot data (PPD). Model fit and accuracy are described by the correlation coefficient of the cross-validated predictions (R^2), Theil's uncertainty coefficient (Theil's U), root mean squared error of prediction (RMSEP (%)), the percent of predicted values below a mean prediction error of 30% (< MPE (%)) and the number of PLSR components (ncomps). The value range of the RPD is described by the minimum (min), maximum (max), mean ± standard deviation (SD).

Category	Functional type	PLSR model (RPD)					Value range (RPD)		External validation (PPD)			
		R^2	Theil's U	RMSEP (%)	<MPE (%)	ncomps	min - max	mean ± SD	R^2	Theil's U	RMSEP (%)	<MPE (%)
Life form	Graminoids	0.56	0.17	17.3	58.5	12	2.6 - 96.5	46.3 ± 26.1	-0.03	0.27	28.8	38.9
(cover %)	Forbs	0.52	0.20	13.0	45.1	11	0.7 - 92.0	27.4 ± 18.7	0.18	0.24	18.2	63.9
	Legumes	-0.06	0.50	6.2	23.2	1	0.0 - 31.0	4.6 ± 6.1	-0.03	0.70	21.7	19.4
	Forbs + Legumes	0.50	0.19	14.1	51.2	10	0.8 - 92.0	32.0 ± 20.2	0.08	0.28	29.5	50.0
	Shrubs	0.47	0.31	8.8	23.2	12	0.0 - 57.5	8.7 ± 12.2	0.19	0.41	10.3	30.6
Growth form	Tussocks	0.27	0.30	20.2	31.7	12	0.0 - 90.0	25.1 ± 23.9	-0.03	0.47	24.8	16.7
(cover %)	Stolons	0.09	0.36	18.3	28.1	2	0.5 - 90.5	21.2 ± 19.3	0.10	0.32	19.2	27.8
Strategy type	C strategist	0.45	0.12	0.27	82.9	5	1.39 - 1.73	1.09 ± 0.37	0.37	0.11	0.26	83.3
(scores)	S strategist	0.52	0.11	0.24	84.1	7	0.93 - 1.54	1.03 ± 0.35	0.28	0.11	0.25	86.1
	R strategist	0.39	0.20	0.15	54.9	10	0.03 - 0.88	0.33 ± 0.19	0.36	0.25	0.23	50.0
Indicator	Soil nutrients	0.62	0.06	0.34	99.8	7	1.71 - 4.06	2.60 ± 0.55	0.58	0.08	0.44	94.4
value	Soil moisture	0.40	0.08	0.43	100	10	1.93 - 4.10	2.68 ± 0.56	0.38	0.08	0.44	91.7
	Light	0.16	0.04	0.34	100	1	3.04 - 4.73	3.82 ± 0.37	0.24	0.03	0.21	100
	Mowing tolerance	0.28	0.08	0.40	99.8	5	2.03 - 3.49	2.59 ± 0.47	0.30	0.09	0.48	88.9

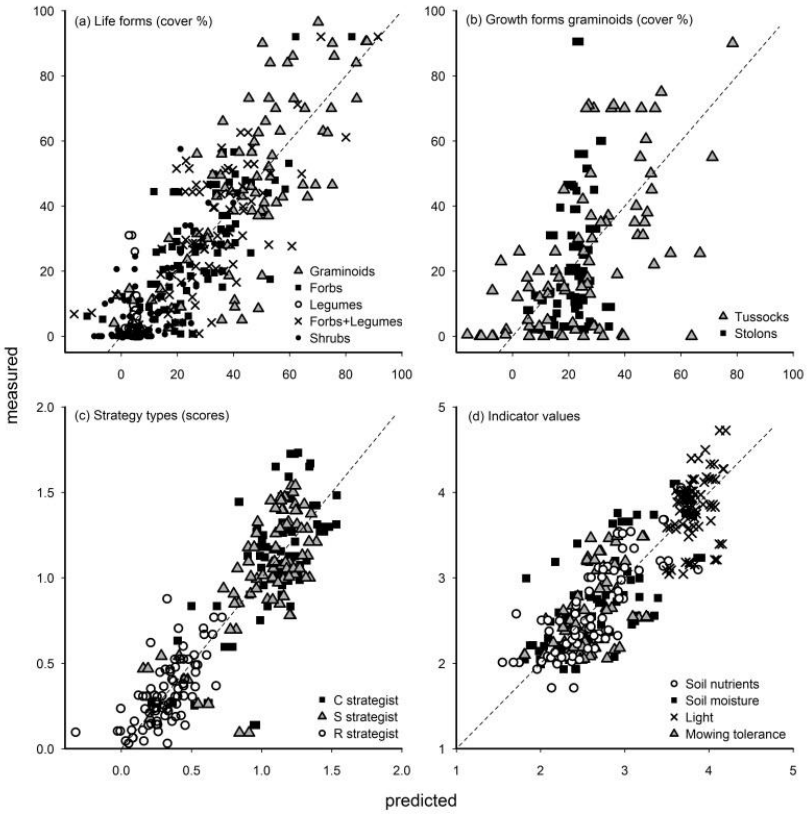


Figure 3.3 Performance of the PLSR models predicting (a) plant life forms (graminoids, forbs, legumes, forbs + legumes combined, shrubs; cover %), (b) growth forms of graminoids (tussocks, stolons; cover %), (c) CSR strategy types (competitor (C), stress-tolerator (S), ruderal (R); scores), and (d) indicator values (soil nutrients, soil moisture, light, mowing tolerance) using research plot data (RPD). The dotted line represents the 1:1 line, n=50 for all graphs.

C strategists are generally found in low stress (sufficient nutrients, water, light) and low disturbance (little damage to plant material) environments (Hodgson et al. 1999), where they invest much in photosynthesis and grow fast (Grime et al. 1997). S strategists are indicative for low disturbance but high stress environments, where they grow slow, invest little in photosynthesis and seeds, but live long. R strategists, in turn, are indicative for environments with high disturbances, where they grow fast, invest much in photosynthesis and seeds, but are short-lived (Grime 1977). As the main CO_2-fixing enzyme RuBisCO (Ribulose-1,5-bisphosphate carboxylase-oxygenase) accounts for 30% to 60% of the total N content in plants (Elvidge 1990), photosynthetic capacity is positively linked to plant N content. However, plants generally trade off their investment in photosynthesis against life span and structural components of leaves (Reich et al. 1992). Thus, fast-growing (C and R strategy types) and/or short-lived plants (R strategy type) are expected to have high N content, but less structural components (low DM and/or fiber content). Long-lived plants (S strategy type) are, in contrast, expected to invest more in structural components but less in photosynthesis. These relationships were confirmed by the correlation structure between CSR strategy types and vegetation community traits (Fig. 3.1), which allowed us to detect CSR strategy types in the spectral response.

The alpine grasslands in the SNP are predominantly single-layered (79.4 ± 23.1% total vegetation cover in the RPD) and restricted in growth due to a short growing season, relatively low precipitation, high solar radiation and high consumption rates of herbivores. Thus, species with high light indicator values dominate the SNP's grasslands, which was correctly predicted by our PLSR models.

Predicting PFTs within the vegetation community allows detecting fine-scale variations in ecosystem composition and functioning (Kokaly *et al.* 2009). While PFTs conceal the presence of single species, which can be essential for beta-diversity assessments, environmental change is generally first reflected in abundance changes rather than changes in presence or absence of a single plant species (Diekmann 2003). Spectroscopic methods have been criticized to be non-transferable among sites (Martens 2001). However, our results show that PLSR techniques can be extended to larger areas by including predictor variables covering the entire expected variability of PFTs and the spectral response. Thus, it might become possible to use PFTs to assess ecosystem functions and services at large spatial scales, e.g. by joining spectral, PFT and plant trait databases. The launches of new remote sensing instruments, in particular the spaceborne imaging spectrometers EnMAP (planned in 2018, EOC of DLR 2015), PRISMA (planned in 2017, Lopinto & Ananasso 2013) and HyspIRI (planned after 2022, NASA 2012), could thus provide the opportunity to bring this functional approach to diversity to the global scale. Future research could focus on how many and which PFTs are needed to provide specific ecosystem functions and which of them should be prioritized in decision making processes. The combination of global datasets of functional diversity with climatic, demographic and socioeconomic data could then be used to quantify the responses of ecosystems to management, to test the sensitivity of ecosystems to specific drivers or global change scenarios, and to predict long term consequences of altered ecosystem conditions including trade-offs between different ecosystem services (MEA 2005).

Summarized, our results demonstrated that relevé data can be combined with imaging spectroscopy data to model and predict a variety of PFTs in highly heterogeneous grasslands using PLSR coefficients as proxies for community level FTTs. Linking the vegetation's functional and spectral signatures could potentially facilitate global ecosystem services assessment as both share advantageous characteristics: i) they are generalizable and thus can be used across large spatial scales, ii) they are integrative and thus enable to capture not only single factors, but also processes, iii) both are directly linked to structural and biochemical vegetation traits ensuring their interpretability, and iv) they can be used on an ecologically relevant and practicable scale: the vegetation community level.

4 FORAGING ECOLOGY OF THREE SYMPATRIC UNGULATE SPECIES – BEHAVIOURAL AND RESOURCE MAPS INDICATE DIFFERENCES BETWEEN CHAMOIS, IBEX AND RED DEER

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Authors' contributions: AKS participated in designing the study, planned and carried out field work, performed the statistical analysis, drafted the initial version of the manuscript, coordinated manuscript preparation and wrote the manuscript. MS designed the study, planned and carried out field work, provided statistical support and wrote the manuscript. PA provided statistical support and provided comments to the manuscript. MES designed the study and wrote the manuscript. MK designed the study, pre-processed IS data and wrote the manuscript. RH designed the study and provided comments to the manuscript. ACR designed the study, planned and carried out field work, provided statistical support and wrote the manuscript. All authors read and approved the final manuscript.

Abstract

Background: The spatial distribution of forage resources is a major driver of animal movement patterns. Understanding where animals forage is important for the conservation of multi-species communities, since interspecific competition can emerge if different species use the same depletable resources. However, determining forage resources in a spatially continuous fashion in alpine grasslands at high spatial resolution was challenging up to now, because terrain heterogeneity causes vegetation characteristics to vary at small spatial scales, and methods for detection of behavioural phases in animal movement patterns were not widely available. We delineated areas coupled to the foraging behaviour of three sympatric ungulate species (chamois, ibex, red deer) using Time Local Convex Hull (T-LoCoH), a non-parametric utilisation distribution method incorporating spatial and temporal autocorrelation structure of GPS data. We used resource maps of plant biomass and plant nitrogen content derived from high-resolution airborne imaging spectroscopy data, and multinomial logistic regression to compare the foraging areas of the three ungulate species.

We found significant differences in plant biomass and plant nitrogen content between the core foraging areas of chamois, ibex and red deer. Core foraging areas of chamois were characterised by low plant biomass and low to medium plant nitrogen content. Core foraging areas of ibex were, in contrast, characterised by high plant nitrogen content, but varied in plant biomass, and core foraging areas of red deer had high plant biomass, but varied in plant nitrogen content.

Previous studies carried out in the same study area found no difference in forage consumed by chamois, ibex and red deer. Methodologically, those studies were based on micro-histological analysis of plant fragments identifying them to plant family or functional type level. However, vegetation properties such as productivity (biomass) or plant nutrient content can vary within vegetation communities, especially in highly heterogeneous landscapes. Thus, the combination of high spatial resolution resource maps with a utilisation distribution method allowing to generate behavioural maps (T-LoCoH) provides new insights into the foraging ecology of the three sympatric species, important for their conservation and to monitor expected future changes.

Background

How ecologically similar species coexist in a shared habitat is a fundamental question in ecology (Hutchinson 1959). Resource ecology provides the basis for understanding multi-species assemblages as it deals with plant-nutrient relationships, interactions between consumers and resources and interactions among consumers (Van Langevelde & Prins 2008). Foraging is the central process in resource ecology as it leads to growth, survival and reproduction of the animal and thus, ultimately influences its fitness (Van Langevelde & Prins 2008). Ungulates forage selectively (Hanley 1997) and are not only influenced by vegetation and landscape structure, but are themselves major drivers of landscape heterogeneity (McNaughton 1979; McNaughton *et al.* 1997; Risch & Frank 2006; De Knegt *et al.* 2008; De Jager & Pastor 2009). Additionally, ungulates affect the abundance and population dynamics of other species, ranging from herbivores (Coughenour 1991) to soil decomposers (Wardle *et al.* 2004) which in turn feed back to vegetation composition and structure. These traits make the spatial distribution and foraging ecology of ungulates an important issue in wildlife management, nature protection and landscape conservation (Bailey *et al.* 1996).

The diversity of ungulate communities is often explained by differences in their dietary niches (Hofmann 1989). Most studies have investigated forage selection based on plant family or functional type (e.g. graminoids, forbs, shrubs) level and have used either direct observations (Gordon & Illius 1989; Brambilla *et al.* 2006), fence experiments (Gordon & Illius 1989; Hülber *et al.* 2005) or micro-histological analysis of faecal pellets (Klansek *et al.* 1995; Bagchi *et al.* 2003; Bertolino *et al.* 2009; La Morgia & Bassano 2009; Lovari *et al.* 2014). Thus, ungulates are traditionally categorised according to their feeding types as grazers, mixed feeders or browsers (concentrate selectors) (Hofmann 1989; Hanley 1997). Previous studies defined chamois (*Rupicapra rupicapra* L.), ibex (*Capra ibex* L.) and red deer (*Cervus elaphus* L.) as mixed feeders, with chamois being closer to browsers, ibex closer to grazers and red deer in between (Gordon & Illius 1989; Hofmann 1989; Pérez-Barbería *et al.* 2001). Such similarity of dietary niches would imply high potential for competition among the three species, especially when population numbers are high. In the Trupchun valley of the Swiss National Park (SNP) population sizes of sympatric chamois, ibex and red deer are amongst the highest in central Europe. Previous studies in our study area investigated the forage composition of these three species using micro-histological analysis of faecal pellets and found no significant differences in the proportions of grasses, sedges, forbs and woody species consumed during spring and summer (Trutmann 2009; Zingg 2009; Anderwald *et al.* 2013).

However, large variations in forage composition at the plant species and plant family level were not only reported between, but also within ungulate species (e.g. for deer species see Hanley 1997) suggesting flexibility in their dietary choices. Additionally, plant species within a vegetation type can strongly differ in growth form and nutritious value resulting from small scale heterogeneity of microclimate and soil, which is especially pronounced in alpine landscapes (Duparc *et al.* 2013). Thus, vegetation type classifications might conceal the heterogeneity of forage resources (Blix *et al.* 2014). High-resolution remote sensing has demonstrated the potential to detect environmental heterogeneity (Kerr & Ostrovsky 2003; Aplin 2005) at a spatial scale fine enough to be relevant for foraging animals (Hanley 1997; Blix *et al.* 2014; Kneubühler *et al.* 2014). Advanced observational approaches such as imaging spectroscopy (IS; Schaepman *et al.* 2009; Schaepman *et al.* 2015) make it possible to detect changes in plant biochemical and biophysical composition (Ustin *et al.* 2004; Aplin 2005; Wang *et al.* 2010), and plant species distribution (Pottier *et al.* 2014). Plant biomass and plant nitrogen (N) content are vegetation characteristics important for forage resource selection in ungulates (McNaughton 1988; Langvatn & Hanley 1993; Wilmshurst & Fryxell 1995; Smallegange &

Brunsting 2002; Skidmore *et al.* 2010 and have already been mapped successfully using IS in heterogeneous grassland ecosystems (Mutanga & Skidmore 2004; Cho & Skidmore 2009; Skidmore *et al.* 2010; Schweiger *et al.* 2015a).

The home range (HR) of an animal is the area traversed by the individual during its normal activities of food gathering, mating and caring for offspring (Burt 1943). Advances in global positioning system (GPS) technology have made it possible to collect large amounts of location data (Cagnacci *et al.* 2010; Tomkiewicz *et al.* 2010) and several HR estimators (polygon methods) - from minimum convex polygons (MCP) to alpha hulls (Burgman & Fox 2003), kernel density estimators (KDE) and local convex hulls (LoCoH) (Getz & Wilmers 2004).

Traditional HR estimators have been criticised for treating locations as spatially and temporally independent, an assumption that can only be fulfilled when data are collected either at random (Otis & White 1999) or at time intervals long enough to allow an animal to move to any place within its HR (McNay *et al.* 1994). However, it has been argued that efforts to handle spatial autocorrelation, which can be an intrinsic data attribute (Fieberg *et al.* 2010), have drawn attention away from more important questions in HR analysis (Fieberg 2007). Instead of removing spatial autocorrelation, which has been shown to be of limited relevance for HR estimators (e.g. KDE) it can be used as a source of biological information and therefore be incorporated in models of animal movement and space use (Solla *et al.* 1999).

Similarly, polygon methods have been criticised for giving only limited information about the species' biology when focussing on the perimeter (size and shape) of an HR. Thus, additional insights into the species' biology might be gained (i.e. what the animal did and where) by using spatial and temporal autocorrelation to delineate areas coupled to the animal's behaviour (Otis & White 1999). During the last decade, models of space use incorporating temporal autocorrelation of GPS data became more widely available, including (dynamic) Brownian bridge movement models (BBMM; Horne *et al.* 2007; Kranstauber *et al.* 2012), Levy flight movement models (Viswanathan *et al.* 1999), movement based kernel density estimators (MKDE; Benhamou & Riotte-Lambert 2012) and time geography methods (Long & Nelson 2012). Similarly, behavioural models (models of time-use) that take advantage of the temporal autocorrelation of GPS data, such as cognitive models (Bartumeus & Levin 2008) or state-space models (Patterson *et al.* 2008) developed.

One of the few methods that take both spatial and temporal autocorrelation of GPS data into account is the Time Local Convex Hull approach (T-LoCoH; Lyons *et al.* 2013). T-LoCoH introduces time-scaled distance (TSD), which measures the distance between two points in both space (using the x/y coordinates) and time (using timestamps) allowing to calculate time-use metrics, such as directionality of movement, duration of stay or revisitation rate of a specific area (Lyons *et al.* 2013). These metrics can be used to generate behavioural maps serving as proxies to delineate migration corridors, resting or foraging areas. Core foraging areas have been defined as regions within an HR that are most heavily used for foraging (Brown & Sherry 2008) and have been approximated by taking the 10% to 50% isopleths of an animal's utility distribution (UD; see Bontadina *et al.* 2002; Brown & Sherry 2008). T-LoCoH´s ability to detect behavioural phases using the temporal and spatial autocorrelation structure of GPS data (Lyons *et al.* 2013) fills an important gap in HR analyses (Fieberg *et al.* 2010).

Ungulates are mobile, have accurate spatial memory (Bailey *et al.* 1996), spend most of their time feeding (Hudson & Frank 1987) and allocate their time according to the resources available (Hamel & Côté 2008; De Jager & Pastor 2009). Thus, areas frequently revisited by the animals can be expected to contain important forage resources. Thanks to the SNP's long term monitoring and behavioural studies (Hofmann 1971; Hegglin 1996) we know that ungulates in the SNP follow daily movement patterns between foraging sites and are active during most time of the day, likely caused by limited

disturbances (strong protection status, absence of predators). Red deer are known to follow a bimodal diurnal rhythm (peaks around sunrise and sunset) in areas strongly influenced by human activities (Georgii & Schröder 1983) while behaving polyphasal (several activity peaks during day and night) when human disturbance is low (Kamler *et al.* 2007).

The goal of our study was to investigate the potential of combining high-resolution remote sensing data with a HR estimator incorporating the behavioural information contained in GPS data for studying a classical issue in resource ecology, resource partitioning between sympatric species. We used GPS data and T-LoCoHs' revisitation index to delineate the core foraging areas of the three ungulate species, chamois, ibex and red deer, co-occurring at high population densities in the Trupchun valley of the SNP and airborne IS data to map plant biomass (forage quantity) and plant N content (forage quality) at 2 x 2 m spatial resolution. We compared vegetation characteristics in the core foraging areas of the three ungulate species with multinomial logistic regression and related our results to previous studies examining their diet composition.

Methods

Study area

Our study was carried out in the Trupchun valley (46.6° N, 10.08° E) of the SNP, encompassing approximately 22 km^2 close to the Italian border. Elevation in Trupchun valley ranges from 1775 to 3145 meter above sea level (m a.s.l.), the average annual temperature in the SNP is 0.9 ± 0.5 °C (mean ± SD) and the mean precipitation is 754 ± 164 mm (2004–2013, recorded at the park's weather station at 1977 m a.s.l.) (MeteoSwiss 2013). The plant' growing season lasts from mid May until mid September. The Trupchun valley is known for its high numbers of co-occurring ungulates; population estimates between 9 - 10 chamois/km^2, 10 - 11 ibex/km^2 and 25 - 31 red deer/km^2 were reported in 2010-2013 (ENPK 2010-2013).

Vegetation data

We collected vegetation data allowing validation of IS data based models in 51 (2010, 2011) to 100 plots (2012, 2013), covering the entire range of exposition, altitude, productivity and plant species composition in the Trupchun valley. These plots were 6 x 6 m in size, homogenous in vegetation cover and species composition and were grouped into five clusters to enable harvesting within a short time frame after the APEX overflight (approximately four hours; see Schweiger *et al.* 2015a) for details). Georeferencing of the plots was performed using a high-precision GNSS (Global Navigation Satellite System) receiver (Leica 1200+, Leica Geosystems, Heerbrugg, Switzerland) with measurement accuracy < 1 cm. On the day of overflight, 1 m^2 of vegetation was clipped in the centre of each plot and immediately sealed into plastic bags. We weighed the samples the same day to determine fresh weight of plant biomass. Then the samples were dried at 65° C and milled to pass a 0.5 mm screen (Pulverisette 16, Fritsch, Idar-Oberstein, Germany). One third of the vegetation samples were chemically analysed for total plant N and plant NDF (neutral detergent fibre) content using standard laboratory methods (TruSpec CN analyser Leco Corp., St Joseph, MI, USA; Fibre Analyser 200, Ankom Technology, NY, USA). Plant NDF content is a widely used indicator of forage quality and important for ruminal function in ungulates (Van Soest 1994). The reflectance spectra of the vegetation samples were measured using a laboratory near-infrared reflectance spectrometer (NIRS; Multi-purpose near-infrared reflectance spectrometer (NIR-MPA), Bruker Optics, Switzerland) and chemically analysed samples were subsequently used to calibrate models for predicting plant N content and plant NDF

content of all vegetation samples. NIRS models achieved predictive accuracies of R^2 = 0.93 for plant N and R^2 = 0.81 for plant NDF content. Since we found strong correlation between plant N content and plant NDF content (R^2 = - 0.61, $p < 0.001$), we excluded plant NDF content from further analysis. When comparing the vegetation characteristics in the plots sampled in all four years (n = 25), using Wilcoxon rank sum tests for pairwise comparisons, no significant differences regarding plant biomass (all $p \geq 0.19$) and plant N content (all $p \geq 0.35$) were found. This allowed us to combine GPS data of the animals collected in different years (but always within 43 days of the APEX flight) with the corresponding IS data sets.

Imaging spectroscopy data

Imaging spectroscopy (IS) data were collected on June 24, 2010, June 26, 2011, June 29, 2012 and July 12, 2013 using the airborne imaging spectrometer APEX (Jehle *et al.* 2010; Schaepman *et al.* 2015) mounted on a propeller aircraft (Dornier DO-228) operated by the German Aerospace Centre (DLR). APEX covers the wavelength region between 380 nm and 2500 nm in 334 reconfigurable spectral bands. After removing noisy bands, 285 (2010), 301 (2011), 299 (2012) and 284 (2013) spectral bands remained for analysis. Ground pixel size depended on flight altitude, but was resampled to 2 x 2 m. APEX IS data were geometrically and atmospherically corrected using the software packages PARGE (Schläpfer & Richter 2002) and ATCOR-4 (Richter & Schläpfer 2002), based on the atmospheric radiative transfer code MODTRAN-5. Geometric mis-registration of the orthorectified data was evaluated using ground-based differential global positioning system (DGPS) measurements and was found to be less than one pixel (± 2 m) in flat terrain (Damm *et al.* 2012) and up to two pixels (± 4 m) on steep slopes (A. Damm, personal communication). Generally, IS data collected at different times are not comparable due to differences in sun angle and atmospheric conditions resulting in varying surface anisotropy. Therefore, we used APEX IS data and ground reference vegetation data to model forage quantity and quality for each year separately. Since reference plots measured 6 x 6 m and APEX pixel size was 2 x 2 m, a 3 x 3 pixel aggregation scheme was defined to extract the reflectance values from the IS data per plot.

We calculated simple ratios indices (SRI = band i/band j) for all possible band combinations based on the average reflectance of the 9 aggregated pixels per plot and determined the correlation between plant biomass ($g.m^{-2}$) and plant N (%) content and the SRI using Pearson's correlation coefficient (R^2). Next, we used the SRI's with the 100 highest correlations (according to R^2) as input to model plant biomass and plant N content with linear, exponential and second order polynomial functions and validated the models using leave-one out cross validation (see also Schweiger *et al.* 2015a). We selected the best model according to Akaike´s Information Criterion (AIC) and evaluated model fit with Theil's uncertainty coefficient (Theil's U). Compared to Pearson correlation, Theil's U has the advantage of taking deviations of the slope from its ideal value of 1 and deviations of the intercept from its ideal value of 0 into account (Smith & Rose 1995). Theil's U normalizes the sum of the squared prediction errors between observed and predicted values to a value between zero and one, with zero indicating perfect agreement (Smith & Rose 1995). Generally, values of Theil's U < 0.2 indicate high, values between 0.2 and 0.4 moderately high predictive power. Due to their frequent use, we also added R^2 values in our text and graphs. Additionally, we determined predictive accuracy by calculating the root mean squared error of prediction (RMSE) and the proportion of samples predicted within less than 20% RMSE. Finally, we applied the best models to predict and map plant biomass and plant N content in all 2 x 2 m raster cells of the grasslands in Trupchun valley. Since our models were designed to predict plant biomass and plant N content only in grasslands, we used linear spectral

unmixing (LSU) and applied a 50% threshold to exclude areas dominated by forest, rock, snow or water from mapping (Roberts *et al.* 1993). IS data were prepared using ENVI (version 4.7; Exelis Visual Information Solutions, Boulder, CO, US). All analyses were conducted in R (version 3.0.2; R Core Team 2013). For the map layout we used ArcGIS (version 10.1; Environmental Systems Research Institute, Redlands, CA, US).

GPS data collection

To match the temporal scale of IS data collection we used GPS data from five chamois (two in 2011, one in 2012, two in 2013), seven ibex (four in 2010, three in 2013) and two red deer (both in 2013) recorded within three weeks before and three weeks after the APEX IS flights (total of 43 days per year). All animals were caught and handled by SNP rangers experienced in the procedures and regularly supervised by a veterinarian. Chamois and female ibex were caught in box traps and marked without narcosis. Red deer and male ibex were darted and injected with 1 ml to 3 ml Hellabrunner Mischung (125 mg Xylazin + 100 mg Ketamin per ml), dependent on body weight. The animals were released within 30 minutes after an injection of 1 ml to 3 ml Antipamezol, an antagonistic drug. The animals were equipped with GPS PLUS collars (Vectronic Aerospace GmbH, Berlin, Germany). The fix rate was set to either four or two hours, but was resampled to the common interval of four hours during data preparation. We performed a GPS accuracy test, placing two collars at six georeferenced (Leica GNSS 1200+, see above) locations, two in the main valley, two in the forest and two in the grasslands of Trupchun valley. We placed the collars around wooden frames with heights ranging from 120 cm to 140 cm and rotated the collars between the locations on a weekly basis. The location error of the collars was 11.3 ± 4.7 m (mean ± SD; [= SQRT ((SD (x-coordinate)^2) + (SD (y-coordinate)^2))]). If the animal was captured or recaptured during the 43 day time window around the APEX flights, the first and last days of data collection were excluded from analysis. GPS data were screened for unrealistic movement following the method of Bjørneraas *et al.* (2010) with limiting parameters set to α = 1.5 km/h and cos θ = -0.97 (velocity and turning angle defining erroneous turnarounds, i.e. spikes in the data), μ = 50 km (possible distance travelled within 20 h) and Δ = 200 km (distance impossible to travel within 20 h; for details see Bjørneraas *et al.* 2010).

Behavioural maps

We used the T-LoCoH package in R (Lyons *et al.* 2014) a non-parametric UD method to construct behavioural maps (Lyons *et al.* 2013) that serve as proxy to delineate the core foraging areas of the three ungulate species. T-LoCoH models space use by constructing local MCP's or hulls around each data point, which are then sorted and progressively merged to form isopleths. Sorting of the hulls can be based on different time-use metrics that serve as proxies for the animals' behaviour, such as duration of stay, directionality of movement and revisitation rates. The time-stamp of each location is incorporated in both, the selection of nearest neighbours for local hull construction and the sorting of the hulls. For hull construction, two points have to be close in time and in space to be considered nearest neighbours. T-LoCoH introduces a distance function that transforms a unit of time into a unit of distance, called time-scaled distance (TSD). The time and space components of TSD are weighted by setting parameter 's'. To make comparisons between the animals possible, we used the same process for all individuals and species and set 's' to a consistent proportion of 60% time selected hulls (Lyons *et al.* 2013; Dürr & Ward 2014).

The number of nearest neighbours can be defined by selecting the 'k' closest points in space and time ('k-method'), the points within a defined time-scaled radius 'r' ('r-method') or by identifying the nearest neighbours up to a cumulative distance 'a' in space and time ('a-method'). We decided to use the 'a-method' as this method is better suited for studies where both, high and low point densities of GPS locations can be expected (Getz & Wilmers 2004). As before, we used the same process to define parameter 'a' for all individuals of all species. We set parameter 'a' to a cumulative distance that stabilised the isopleths' edge to area ratio (Lyons et al. 2013; Dürr & Ward 2014) before creating a jump in the isopleths' area, thus balancing type I (including area that is not used) and type II errors (omitting area that is used; Lyons 2014). Since absolute values for the optimal 'a' across all individuals of a specific ungulate species were very close, it was reasonable to use the same value for 'a' for all three species. While there are guidelines available for selecting the weight placed on the time-component ('s'-value) and the threshold for nearest neighbour selection ('a'-value; Lyons *et al.* 2013), the parameters for hull sorting and the isopleths' threshold have to be based on the aim of the study and the knowledge of the animals' ecology. In our study area, the three ungulate species show distinct diurnal movement patterns. They are known to regularly return to the same areas for foraging, ruminating and resting and have multiple activity peaks per day (Hofmann 1971; Hegglin 1996). We therefore calculated the revisitation rate for each hull based on an inter-visit gap (IVG, time to pass for an observation to count as a separate visit) of 12 hours, sorted the hulls according to the mean number of separate visits normalised (NNSV) and merged them until 30% of all points were included (creating the 30% isopleths). While it is likely crucial to limit type II errors (omitting areas important for a species) in conservation projects (e.g. the delineation of protected areas), studies of animal behaviour profit from limiting type I errors (including area that is not used by the species) to detect the patterns of interest. Thus we decided to choose a tight threshold, i.e. the 30% isopleths, to delineate the animals' core foraging areas.

Species comparison

We fitted multinomial logistic regression models using the three ungulate species as the response and plant biomass and plant N content in the animals' core foraging areas as predictor variables. We rescaled plant biomass to a level similar to plant N content by dividing all biomass values by 100 (BiomRS = Biomass/100). As candidate models we chose i) the two models containing only one predictor variable (plant biomass or plant N content), ii) the main effects model containing both terms (plant biomass and plant N content), iii) the model including both terms plus their interaction and iv) the intercept-only model. We selected the best model based on differences of AIC (Δ AIC) and confirmed our selection using the likelihood ratio test.

To evaluate model fit we calculated the Hosmer-Lemeshow goodness-of-fit statistic and the area under curve (AUC) of the receiver-operating characteristic (ROC) for each of the two logits separately (Hosmer *et al.* 2013). The ROC is obtained by plotting all sensitivity values (true-positive fraction) on the y-axis against their equivalent 1-specificity values (false-positive fraction) for all thresholds on the x-axis. Thus, this measure of overall accuracy is independent of any threshold (Fielding & Bell 1997). AUC values between 0.7 and 0.8 indicate good, values between 0.8 and 0.9 excellent discriminative ability (Pearce & Ferrier 2000). We assessed the sensitivity of our results with regard to the size of the animals' core foraging areas by re-running the analysis after adding and subtracting a 6 m buffer to the core foraging areas, respectively, and tested the hypothesis of equality of the model coefficients. For analyses and graphs we used the packages nnet (Venables & Ripley 2002), pROC (Robin *et al.* 2011) and effects (Fox & Hong 2009) in R (R Core Team 2013).

Results

The SRI models of grassland vegetation developed from APEX IS data predicted plant biomass and plant N content with high to moderately high predictive power (Table 4.1). Generally, the grasslands in the Trupchun valley showed high heterogeneity regarding plant biomass and plant N content (Table 4.2).

Table 4.1 Imaging spectroscopy models predicting fresh weight of plant biomass and plant nitrogen content. Models were generated separately for each year using data from the imaging spectrometer APEX and in situ vegetation data. Model performance is described using Theil's uncertainty coefficient (Theil's U), adjusted Pearson's correlation coefficient (adj. R^2), root mean squared error of prediction (RMSE) and % of predicted values below 20% RMSE (< 20% RMSE (%)).

Year	Model performance	Biomass ($g.m^{-2}$)	Nitrogen (%)
2010	Theil's U	0.19	0.11
	adj. R^2	0.65	0.53
	RMSE	174.37	0.53
	< 20 % RMSE (%)	44.19	62.79
2011	Theil's U	0.15	0.07
	adj. R^2	0.70	0.43
	RSME	155.71	0.28
	< 20 % RMSE (%)	53.57	88.80
2012	Theil's U	0.23	0.07
	adj. R^2	0.49	0.39
	RSME	174.35	0.26
	< 20 % RMSE (%)	36.44	84.48
2013	Theil's U	0.22	0.08
	adj. R^2	0.43	0.36
	RSME	241.30	0.27
	< 20 % RMSE (%)	36.93	81.67

Table 4.2 Resources in Trupchun valley and in core foraging areas of chamois, ibex and red deer. Biomass ($g.m^{-2}$) = fresh weight of plant biomass ($g.m^{-2}$), N (%) = plant nitrogen content (%), SD = standard deviation, min = minimum, max = maximum.

Vegetation Characteristic	Trupchun	Chamois	Ibex	Red Deer
Mean Biomass ($g.m^{-2}$)	295.26	192.28	242.63	276.79
SD Biomass ($g.m^{-2}$)	230.10	84.83	119.75	107.15
Biomass min ($g.m^{-2}$)	0.10	32.48	0.10	83.84
Biomass max ($g.m^{-2}$)	2799.10	667.61	680.30	986.63
Mean Nitrogen (%)	2.11	1.84	2.37	1.78
SD Nitrogen (%)	0.53	0.25	0.64	0.22
Nitrogen min (%)	0.01	1.29	0.97	1.04
Nitrogen max (%)	4.80	2.75	4.75	3.69

The core foraging areas of chamois, ibex and red deer delineated using T-LoCoH's revisitation index (NNSV) were in agreement with the areas where the three ungulate species are frequently observed (SNP, personal communication). Figure 1 shows examples of spatially segregated core foraging areas in the Trupchun valley. We found minor overlaps of the core foraging areas both within and between species, however they occurred at different times of our observation period. The best multinomial logistic regression model included plant biomass, plant N content and their interaction (df = 8, Table 4.3). When comparing the other candidate models to this model (the interaction model), the main effects model reached a Δ AIC of 38.6 (df = 6), the model including only plant N content a Δ AIC of 668.0 (df = 4), the model including only plant biomass a Δ AIC of 2013.1 (df = 4) and the intercept-only model a Δ AIC of 2538.8 for (df = 2). According to likelihood ratio tests, the interaction model performed clearly better (all $p < 0.001$) than all other models. Therefore, we chose the interaction model as our best model. The Hosmer - Lemeshow goodness-of-fit statistic for each of the two logits reached a value of $p < 0.001$ indicating very good model fit. The best model's AUC was 0.82 for logit 1, indicating excellent ability to discriminate between chamois and ibex core foraging areas, and 0.75 for logit 2, indicating good ability to discriminate between chamois and red deer core foraging areas. Sensitivity analysis revealed no significant differences (all $p > 0.25$) between the best models' coefficients for the two logits, neither after increasing, nor after decreasing the animals' core foraging areas by a 6 m buffer (see Additional file 4.1).

Table 4.3 Best multinomial logistic regression models comparing chamois, ibex and red deer core foraging areas
Logit 1 represents the logistic link function for chamois vs. ibex core foraging areas, logit 2 the logistic link function for chamois vs. red deer core foraging areas. Coefficients of the parameters (Coeff) for plant biomass rescaled (BiomRS = fresh weight of plant biomass/100 ($g.m^{-2}$)), plant nitrogen content (N (%)) and their interaction (BiomRS:N), standard errors (SE), Wald Z-statistic values (z) and corresponding p-values (p) are indicated.

	Variable	Coeff	SE	z	p
Logit 1	Intercept	-8.7218	0.5825	-14.9738	0.0000
Chamois vs. Ibex	BiomRS	1.0043	0.2658	3.7786	0.0002
	N	3.6048	0.2898	12.4381	0.0000
	BiomRS:N	-0.1314	0.1369	-0.9602	0.3369
Logit 2					
Chamois vs. Deer	Intercept	2.2434	0.6461	3.4722	0.0005
	BiomRS	-0.1548	0.2731	-0.5670	0.5707
	N	-2.4917	0.3538	-7.0432	0.0000
	BiomRS:N	0.5535	0.1471	3.7640	0.0002

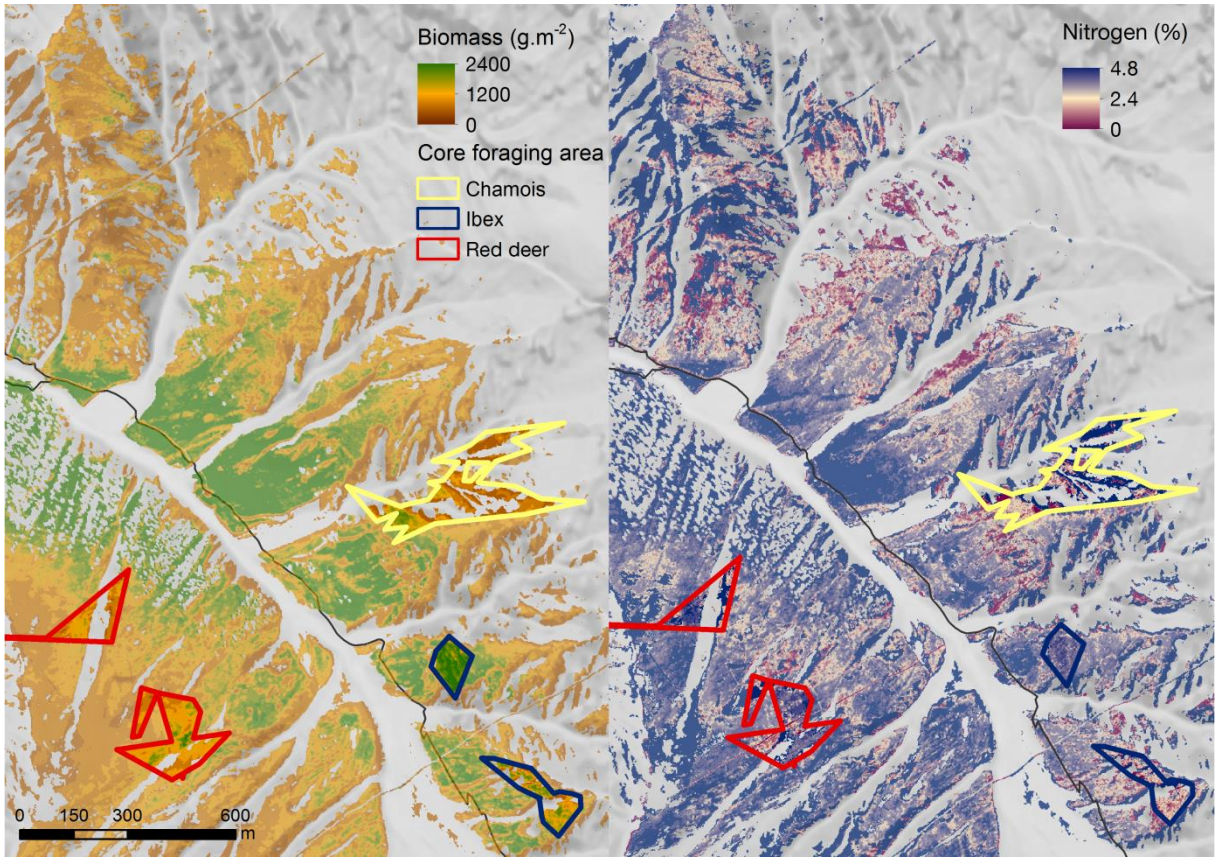

Figure 4.1 Examples of core foraging areas of chamois, ibex and red deer, respectively. Core foraging areas represent the 30% isopleths of T-LoCoH's revisitation index. The map shows fresh weight of plant biomass ($g.m^{-2}$) (left panel) and plant nitrogen content (%) (right panel). Grey colours represent areas covered by forest, rock, snow or water, identified using linear spectral unmixing (LSU) and subsequently excluded from analysis.

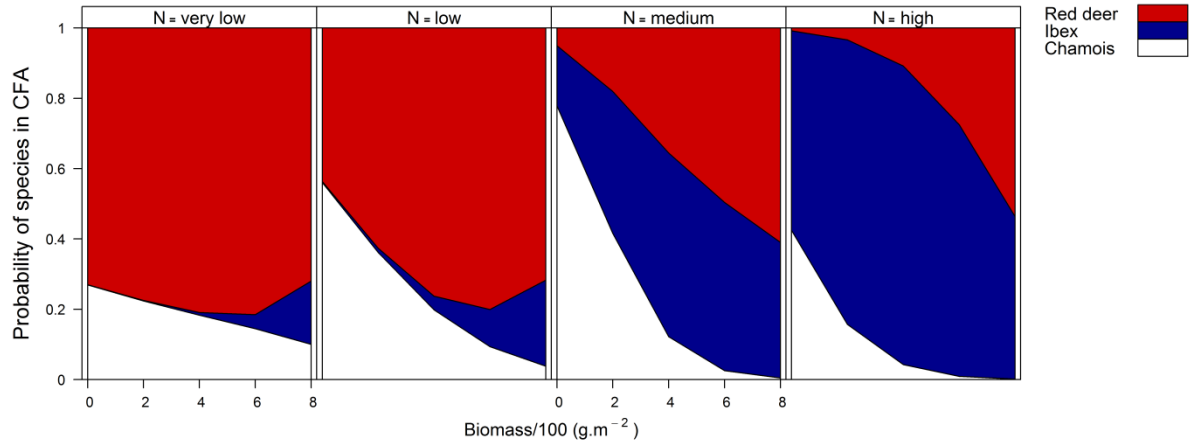

Figure 4.2 Probabilities for de facto use of core foraging areas by red deer, ibex and chamois. Predicted probabilities for chamois, ibex and red deer using core foraging areas (CFA) depending on plant biomass (Biomass/100 ($g.m^{-2}$), x-axis) at increasing levels of plant nitrogen content (very low (< 1%), low (< 2 %), medium (< 2.5 %), high (≥ 2.5 %)) displayed in the panels from left to right. Probabilities were generated from the model in Table 4.3.

The core foraging areas of chamois were characterised by generally low plant biomass (< 200 g.m^{-2} fresh weight, Fig. 4.2, Fig. 4.3), and a low but slightly increased level of plant N content (around 2%, unimodal relationship, Fig. 4.3, Fig. 4.4). In contrast, vegetation in the core foraging areas of ibex was characterised by high plant N content, but variable plant biomass (Fig. 4.2, Fig, 4.4), while vegetation in the core foraging areas of red deer was characterised by high levels of plant biomass, but variable plant N content (Fig. 4.2). Ibex showed a tendency to use areas with the highest plant biomass and plant N content (Fig 4.3). However, the core foraging areas with the highest plant biomass and highest plant N content had an almost 50:50 modelled chance of being used by either ibex or red deer (Fig 4.2).

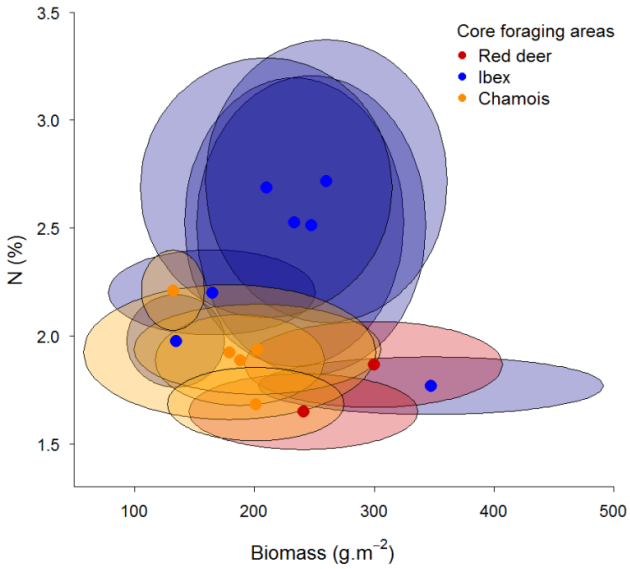

Figure 4.3 Core foraging areas of red deer, ibex and chamois. Core foraging areas of red deer, ibex and chamois regarding plant biomass and plant nitrogen (N) content. Dots represent mean values and the axes of the ellipses standard deviations (SD) in either direction.

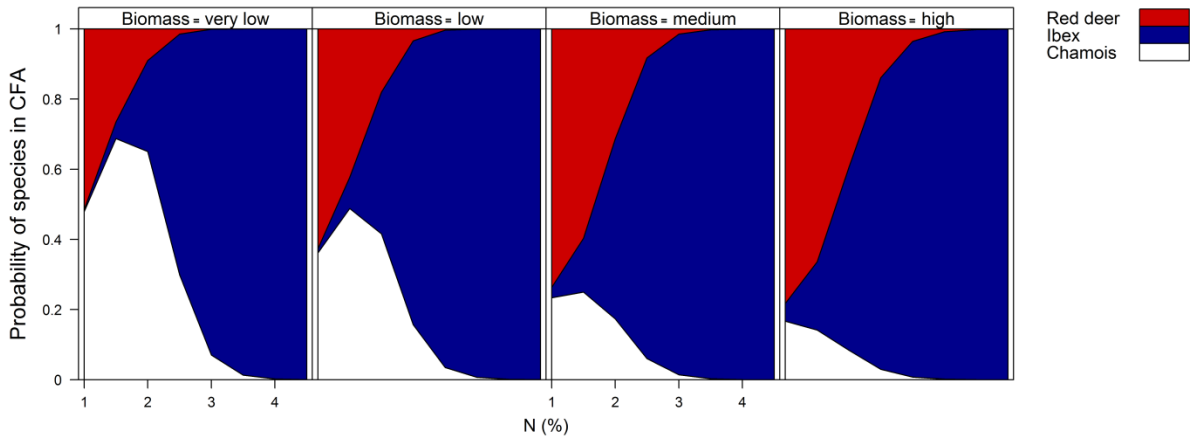

Figure 4.4 Probabilities for de facto use of core foraging areas by red deer, ibex and chamois. Predicted probabilities for chamois, ibex and red deer using core foraging areas (CFA) depending on plant nitrogen content (x-axis) at increasing levels of plant biomass (very low (< 200 g.m^{-2}), low (< 350 g.m^{-2}), medium (< 450 g.m^{-2}), high (≥ 450 g.m^{-2})) displayed in the panels from left to right. Probabilities were generated from the model in Table 4.3.

Discussion

Previous studies conducted in the Trupchun valley found no difference in spring and summer forage composition between chamois, ibex and red deer when using micro-histological analysis of plant fragments in faecal pellets (Trutmann 2009; Zingg 2009; Anderwald *et al.* 2013). Likewise, a large overlap in the diet of chamois and red deer was found when they co-occurred with roe deer (*Capreolus capreolus* L.) in Southern Germany (Schröder & Schröder 1984) with mouflon (*Ovis ammon musimon* Pallas) in the Western Alps (Bertolino *et al.* 2009) and with re-introduced red deer in the Italian Apennine (Lovari *et al.* 2014). While overlap in resource use (of both habitat and forage) is a prerequisite for competition (Putman 1996), it could also be a sign of coexistence between species with no need of specialisation or segregation (De Boer & Prins 1990). Similarly, low overlap in diet and high specialisation may point towards species living in coexistence (Hutchinson 1959) but could also be an effect of active competition, with the species trying to relieve competitive pressure (De Boer & Prins 1990). This makes coexistence and competition extremely difficult to demonstrate in the field and without experimental manipulation (Connell 1980; Putman 1996; Chase & Leibold 2003), and conclusion have to be drawn with care.

The studies mentioned above used micro-histological analyses of faecal pellets and thus identified forage remains at the level of plant functional groups or plant families. However, the ratios of the two main forage components, graminoids and forbs, varied considerably within the ungulate species studied, which suggests that the animals have some flexibility in their dietary choices. Moreover, ungulates are assumed to partition forage resources at levels below the scale of vegetation types Hanley 1997), and several studies confirm that plant biomass, plant nutrient and mineral content are major drivers for the spatial distribution and forage resource selection in ungulates (McNaughton 1988; Langvatn & Hanley 1993; Wilmshurst & Fryxell 1995; Smallegange & Brunsting 2002; Skidmore *et al.* 2010). Therefore, studies investigating forage resource selection in multi-species ungulate communities profit from including forage quantity and quality in their analyses, especially in areas where these vegetation characteristics are expected to vary.

Finding core foraging areas of chamois predominantly where plant biomass was low, red deer core foraging areas where plant biomass was high and ibex in between is in line with traditional feeding type definitions (Hofmann 1989). Regarding body size, chamois as the smallest of our three study species (body weight: 30 - 50 kg) is more limited in terms of forage intake than ibex (body weight: 40 - 150 kg) and red deer (body weight: 60 - 200 kg). However, the differences of plant N content in the core foraging areas of the three species, with chamois foraging in areas with low, ibex in areas with high and red deer in areas with variable plant N content warrant some explanation. Chamois have smaller and less complex rumens resulting in shorter retention time of digesta. This makes them less able to digest fibre, which could indicate that chamois depend on forage with higher plant N content (Hofmann 1989). However, it was found that by comparison to red deer, chamois foraged on lower quality vegetation consisting predominantly of graminoids in areas where food supply was limited (Kamler 2011). Additionally, chamois have been found to select high quality forage in high quality habitats, while foraging in a more generalist pattern in low quality habitats (Brambilla *et al.* 2006). Indeed, as mixed feeders (Hofmann 1989) chamois can be expected to show high plasticity in forage selection, which was supported by our results.

In contrast to chamois, vegetation in the core foraging areas of ibex was characterised by high plant N content and variable plant biomass. Generally, we expected ibex to forage in rocky terrain with little, but nutrient-rich vegetation. While our results suggested that ibex did indeed forage in areas where plant biomass was low but of high nutritious value (high plant N content), we also found ibex core

foraging areas in the highest quality meadows of the Trupchun valley where both plant biomass and plant N content were high. Generally, terrain roughness and slope create a template of risk (Laundré *et al.* 2001; Ripple & Beschta 2004) in which herbivores have to trade-off between resource acquisition (e.g. foraging in high quality habitats, finding mates) and predator avoidance (Wang *et al.* 2009; Anderson *et al.* 2010). Ibex are very good climbers that find protection from predators and the possibility to overview large areas in predominantly rocky terrain with steep slopes. Within the SNP, predators are absent, hunting is prohibited and visitors are obliged to stay on the marked paths. Thus, ibex might have abandoned part of their anti-predator behaviour in favour of maximising forage resource acquisition. Visual observations (SNP, unpublished observations) confirm that the rather flat, high quality meadows are regularly visited by ibex, where they forage together with red deer and occasionally also chamois.

The core foraging areas of red deer were always located on the rather flat meadows where the animals are expected to be able to cover their forage intake needs as plant biomass is high. Red deer inhabit predominantly open, flat terrain, have good running skills and thus withdraw themselves from predator attacks by using areas with high lateral cover, such as areas with forest or tall-growing shrubs. Similar to ibex, red deer might have abandoned part of their anti-predator behaviour as they can be observed grazing, resting and ruminating on the alpine meadows of Trupchun valley during daytime (Hofmann 1971; Hegglin 1996). However, besides the absence of predators and limited disturbance, finding ungulates foraging in open areas with higher plant biomass could also be an effect of high population densities (Coulombe *et al.* 2011). When forage availability in habitats with more protection declines with increasing population numbers, the animals might be forced to use more open terrain for foraging. To assess whether the animals choose the high-quality meadows in Trupchun valley voluntarily (in order to maximise resource acquisition) or if they are forced to use these areas (due to high population numbers) would require a comparison of core foraging areas at variable population densities or in the presence of predators. Wolf, lynx and bear are expected to return to the SNP in the future (Filli 2006), which could have profound impacts on the abundance, population dynamics and spatial distribution of ungulates (Andersen *et al.* 2006). Thus, our results provide an important basis against which to assess future changes.

Due to the fixed dates of the APEX IS data acquisition, the results of our study represent the animals' behaviour during a specific time, i.e. during early summer. However, forage quantity and quality are expected to influence ungulate movement patterns in our study area in particular during this time of the year (peak of the plant growing season), when females have to nourish their offspring, and all individuals have to build up winter reserves. Naturally, the quantity and quality of forage resources will change during the course of the year and therefore also the ungulates' habitat use patterns can be expected to change (Hebblewhite *et al.* 2008; van Beest *et al.* 2011). The habitat use patterns of ungulates are apart from vegetation quantity and quality, also influenced by physical landscape characteristics, such as elevation, aspect and slope, as they can facilitate e.g. effective temperature regulation (Aublet *et al.* 2009; Signer *et al.* 2011; van Beest *et al.* 2011), ease of movement and anti-predator behaviour (Wang *et al.* 2009; Anderson *et al.* 2010). However, vegetation composition and thus the quantity and quality of forage resources depend on microclimate and soil, which are also influenced by elevation, aspect and slope. Disentangling the effects of 'pure' physical landscape characteristics and 'derived' vegetation properties would be challenging but provide important insights into trade-off mechanisms in habitat choice.

The distribution of vegetation quantity and quality influences the space use of herbivores on several spatial and temporal scales (Senft *et al.* 1987; van Beest *et al.* 2011). Large ungulates show HR establishment at the regional or landscape scale, they choose suitable feeding areas and vegetation

communities at the local scale, select vegetation communities of favourable quantity and quality at the patch scale and certain plant species or plant parts at the bite scale (Senft *et al.* 1987; Schweiger *et al.* 2015a). APEX data gathered in this study represents vegetation quantity and quality at the patch scale of 2 x 2 m. It is therefore possible, that some of the ungulate species, especially the smaller chamois, feed more selectively within these patches (Bailey *et al.* 1996; Hanley 1997; Brivio *et al.* 2014). However, visually observing and exactly locating the animals, sampling browsed plants and determining their nutrient content is difficult in an area where access is limited due to challenging terrain and the high protection status. As advances in GPS and remote sensing technology continue, spatially accurate, high-temporal resolution GPS data (e.g. at minute intervals) that allow following the exact movement paths of animals will become more widely available. Combined with temporally flexible, very high spatial resolution remote sensing instruments such as unmanned aerial vehicles (UAV´s; Anderson & Gaston 2013), this would provide opportunities to investigate forage quantity and quality at the individual plant level. Further differentiation might be achieved by not only assessing commonly observable vegetation traits by remote sensing (Homolová *et al.* 2013) but also by adding advanced retrievals of pigment composition (Ustin *et al.* 2009).

Conclusions

We detected significant differences in plant biomass and plant N content in the core foraging areas of sympatric chamois, ibex and red deer when combining resource maps developed from airborne imaging spectroscopy data with behavioural maps developed using the T-LoCoH algorithm: T-LoCoH enables to detect behavioural phases in GPS data by making use of their temporal and spatial autocorrelation. The combination of behavioural and resource maps proved to be valuable for studying a classical issue in resource ecology, resource partitioning between sympatric species. For the future, we expect that the development of remote sensing instruments with increased spatial resolution and temporal flexibility together with highly accurate and short interval GPS systems will continue to deepen our understanding of the foraging ecology of multi-species communities.

Additional file 4.1 - Multinomial logistic regression results after adding and subtracting a 6 m buffer around the animals' core foraging areas (CFA), respectively.

Logit 1 represents the logistic link function for chamois vs. ibex core foraging areas, logit 2 the logistic link function for chamois vs. red deer core foraging areas. Coefficients of the parameters (Coeff) for plant biomass rescaled (BiomRS = fresh weight of plant biomass/100 ($g.m^{-2}$), plant nitrogen content (N (%)) and their interaction (BiomRS:N), standard errors (SE), Wald Z-statistic values (z), corresponding p-values (p) and the p-values for the hypothesis test for equality of the model coefficients (p (Anova)) are indicated.

Original CFA	Variable	Coeff	SE	z	p	
Logit 1	BiomRS	1.0043	0.2658	3.7786	0.0002	
Chamois vs. Ibex	N	3.6048	0.2898	12.4381	0.0000	
	BiomRS:N	-0.1314	0.1369	-0.9602	0.3369	
Logit 2	BiomRS	-0.1548	0.2731	-0.567	0.5707	
Chamois vs. Deer	N	-2.4917	0.3538	-7.0432	0.0000	
	BiomRS:N	0.5535	0.1471	3.764	0.0002	
Original CFA plus 6 m buffer	Variable	Coeff	SE	z	p	p (Anova)
Logit 1	BiomRS	0.6565	0.2147	3.0580	0.0022	0.8542
Chamois vs. Ibex	N	3.0942	0.2245	13.7804	0.0000	0.3736
	BiomRS:N	0.0416	0.1104	0.3768	0.7063	0.4445
Logit 2	BiomRS	-0.1122	0.2240	-0.5010	0.6164	0.6459
Chamois vs. Deer	N	-2.8967	0.2951	-9.8173	0.0000	0.2593
	BiomRS:N	0.5692	0.1208	4.7120	0.0000	0.6289
Original CFA minus 6 m buffer	Variable	Coeff	SE	z	p	p (Anova)
Logit 1	BiomRS	1.2643	0.3302	3.8285	0.0001	0.9947
Chamois vs. Ibex	N	3.9514	0.3674	10.7537	0.0000	0.8007
	BiomRS:N	-0.2640	0.1705	-1.5481	0.1216	0.4863
Logit 2	BiomRS	-0.4466	0.3502	-1.2754	0.2022	0.6022
Chamois vs. Deer	N	-2.4704	0.4506	-5.4824	0.0000	0.4080
	BiomRS:N	0.6697	0.1892	3.5403	0.0004	0.6009

5 SYNTHESIS

5.1 Main findings

Within the main findings of this thesis, the five research questions (Chapter 1.5) are reassessed and discussed as follows.

RQ 1: Can imaging spectroscopy data be used to model plant biomass in highly heterogeneous alpine grasslands?

Imaging spectroscopy and ground reference biomass data were used to develop three biomass models for the grasslands in the SNP, one for the regional study area of the entire SNP (SNP model) and two for the local study areas Val Trupchun (TRU model) and Il Fuorn (FUO model), respectively. Generally, plant biomass was successfully modelled and predicted, with the TRU model performing best (R^2 = 0.60; compared to R^2 = 0.44 for the SNP and R^2 = 0.30 for the FUO model). Plant biomass was modelled following the empirical approach of linking the spectral response to vegetation data collected in field plots and a search routine that identified the best simple ratio (SR = band y/band x) predicting plant biomass using linear, exponential or second order polynomial terms. The best SRs selected as input in our models were located in red and NIR parts of the spectrum, two regions that are regularly used for predicting plant biomass (e.g. Tucker 1979; Mirik *et al.* 2005; Beeri *et al.* 2007; Cho *et al.* 2007; Fava *et al.* 2009). We attribute model precision and accuracy largely to our field data sampling design, which seemed to have been able to capture the entire heterogeneity of the study areas (especially the heterogeneity of study area TRU), which is critical for robust models, validation and accuracy assessment (Lu 2006). The differences in model performance, with the TRU model performing better than both, the FUO and the SNP model, was likely caused by historic land use patterns in study area FUO which have resulted in two distinct vegetation types, nutrient-rich short grass and nutrient-poor tall-grass receiving different grazing intensities (Schütz *et al.* 2003; Schütz *et al.* 2006). Low grazing intensities in the tall-grass resulted in high amounts of non-photosynthetically active vegetation (NPV), whereas high grazing intensities in the short grass seemed to maintain a system similar to grazing lawns (McNaughton 1984; Veldhuis *et al.* 2014) consisting of nutrient rich, photosynthetically active vegetation (PV). Generally, PV is characterized by low fibre and high chlorophyll content, while NPV shows by high fibre and low chlorophyll content. Thus, the structural and biochemical characteristics of NPV and PV were likely too different to allow for accurate predictions of both vegetation types in a single model. Collecting pure spectra of NPV and PV to unmix the spectral response and combining two separate models, one for NPV and one for PV, could possibly improve biomass modelling in this vegetation type. These two distinct vegetation types (NPV-rich tall-grass and PV-rich short-grass) are missing in area TRU, where vegetation is generally more productive and ungulate grazing patterns seem more evenly distributed. Other factors presumably contributing to the better performance of the TRU model were more variability in biomass values, the less heterogeneous distribution of slope and exposure and the higher fraction of total grassland cover.

RQ 2: How much accuracy is lost when extrapolating imaging spectroscopy models for plant biomass to different study areas and different spatial scales?

Unsurprisingly, the three biomass models TRU, FUO and SNP always performed best in the study area and at the spatial scale they were calibrated for. While limited model transferability is a common characteristic of empirical models (Curran 1994), model validation using an external data set revealed that high site specificity of empirical models can also be an advantage. The external validation data was collected from a grassland site within the FUO area and showed a distinct distribution of two vegetation types, short- and tall-grass, characterized by different amounts of PV and NPV. Although its general fit and accuracy (FUO model: $R^2 = 0.30$) was comparable to the TRU (TRU_FUO: $R^2 = 0.28$) and SNP models (SNP_FUO: $R^2 = 0.35$) when transferred to this area, only the local FUO model was able to correctly predict the biomass pattern present. Likewise, a standard broadband index frequently used for biomass estimation, the normalized-difference vegetation index (NDVI; Rouse *et al.* 1974), was not able to correctly capture the biomass pattern, although its fit and accuracy (NDVI_FUO: $R^2 = 0.33$) was comparable to the site specific FUO model. This suggests that standardized approaches might not provide the ideal solution for predicting biomass patterns, particularly in heterogeneous landscapes with distinct vegetation and grazing patterns. Additionally, our results confirm the ability of imaging spectroscopy data to detect subtle changes in narrowband absorption features (Ustin *et al.* 2004; Wang *et al.* 2010), only partially approachable using broadband indices (Asner 1998). It follows that, although empirical models are generally not transferable between sites, they can be superior to standard vegetation indices, given that sufficient ground reference data covering the entire expected variability of the vegetation characteristics of interest are available. Moreover, our results illustrate the importance of external validation data sets to test a model's plausibility.

RQ 3: Can plant functional types (PFTs) be modelled and predicted in heterogeneous alpine grasslands and how is the concept of PFT related to spectral response?

A series of characteristically different PFTs, namely plant life and growth forms, CSR strategy types (competitive, stress-tolerant, ruderal species; Grime 1977), and indicator values for soil nutrients, soil moisture, light and mowing tolerance (Ellenberg *et al.* 1992), were accurately modelled and predicted in the grasslands of SNP (R^2 for life and growth forms = 0.27 - 0.56 (excluding legumes and stolons); R^2 for CSR types = 0.39 - 0.52; R^2 for indicator values = 0.28 - 0.62 (excluding the light indicator value)). This result was confirmed by external model validation, using data from long term vegetation monitoring plots. The PFTs legumes (life form), stolons (growth form) and the indicator value for light availability showed lesser model fit and accuracy, which can be largely attributed to a lower variability in values and thus lacking correlations to spectrally detectable vegetation traits. Analysis of the correlation structure between the PFTs and structural and biochemical vegetation traits, namely plant biomass, plant nitrogen (N), neutral detergent fibre (NDF) and dry matter content revealed how PFTs and vegetation traits are connected with each other. Based on these findings, we propose a conceptual framework for linking PFTs to vegetation traits known to be detectable in the spectral response and suggest partial least squares regression (PLSR) coefficients as proxies to identify PFTs in the spectral signature of the vegetation community. This work encourages the use of PFTs in global assessments of ecosystem services using air- or spaceborne imaging spectrometers.

RQ 4: Can spectroscopic methods be used to model vegetation quality in heterogeneous alpine grasslands?

The quality of vegetation samples, indicated by plant N and plant NDF content, collected in the SNP during four years (2010-2013) were predicted with high precision and accuracy (N: R^2 = 0.93, NDF: R^2 = 0.81) using laboratory near-infrared spectroscopy (NIRS;Foley *et al.* 1998). Empirical models using APEX imaging spectroscopy data, combined with ground reference vegetation data predicted vegetation quantity (plant biomass) and quality (plant N and NDF content), during the same study period with moderate to high accuracies (biomass: R^2 = 0.43 - 0.70, N: R^2 = 0.36 - 0.53; NDF: R^2 = 0.20 - 0.79; see Schweiger *et al.* 2015b for plant biomass and plant N content and Table 5.1 for plant NDF content). Moreover, we found that plant N and NDF content were highly correlated (R^2 = –0.61).

Table 5.1 Predictive modelling of neutral detergent fibre content (NDF). Models were generated separately for each year, using data from the imaging spectrometer APEX and in situ vegetation data. Model performance is described by Theil's uncertainty coefficient (Theil's U), adjusted Pearson's correlation coefficient (adj. R^2), root mean squared error of prediction (RMSE) and % of predicted values below 20% RMSE (< 20% RMSE (%)).

Year	Model performance	NDF (%)
2010	Theil's U	0.04
	adj. R^2	0.67
	RMSE	4.35
	< 20 % RMSE (%)	97.67
2011	Theil's U	0.03
	adj. R^2	0.79
	RSME	2.46
	< 20 % RMSE (%)	100
2012	Theil's U	0.04
	adj. R^2	0.25
	RSME	3.65
	< 20 % RMSE (%)	100
2013	Theil's U	0.04
	adj. R^2	0.20
	RSME	4.29
	< 20 % RMSE (%)	97.22

RQ 5: Are the movement patterns of three sympatric large ungulate species related to vegetation quantity and quality when mapped at high spatial resolution?

The animals' movement patterns were analysed based on the spatial and temporal auto-correlation structure of GPS data (behavioural maps) and resource maps of plant biomass (vegetation quantity) and plant N content (vegetation quality). Due to the correlation between plant N and plant NDF content, maps of plant NDF content were not included in the analysis. The spatial and temporal auto-correlation structure of GPS data allowed to delineate areas coupled to the animals' behavioural patterns (Lyons *et al.* 2013). Analysing the core foraging areas of chamois, ibex and red deer, based on resource maps of plant biomass and plant N content, developed from APEX imaging spectroscopy and ground reference data, revealed significant differences between the species. According to this result, the three species, which co-occur at high population densities, seem to be able to partition forage resources based on forage availability and its nutritious value and thus below the levels of PFTs or plant families. Thus, commonly available vegetation maps based on vegetation types or plant

communities might considerably conceal the heterogeneity of alpine grasslands (Blix *et al.* 2014), as it is likely perceived by the animals, when trading-off their movement and behavioural decisions (Wang *et al.* 2009; Anderson *et al.* 2010). Although, the nutritious value of forage resources was already identified as a major driver of animal movement patterns (McNaughton 1988; Wilmshurst & Fryxell 1995), arguments for competitive interactions between ecologically similar species are regularly based on overlaps in forage resource use, but described at the level of plant families or PFTs (Bagchi *et al.* 2003; Bertolino *et al.* 2009; La Morgia & Bassano 2009). Therefore, resource maps developed from imaging spectroscopy provided valuable additional insights into a classical question in resource ecology, resource partitioning within an animal guild (Gordon & Illius 1989; Putman 1996), reinforcing the view that, while the animals might consume the same plant species, resources can be partitioned based on the amount of forage and its nutrient content.

5.2 General conclusions

The results of this thesis show that structural (plant biomass) and biochemical vegetation traits (plant N and NDF content) can be accurately modelled, predicted and mapped using imaging spectroscopy, even in heterogeneous alpine grasslands. We were able to confirm expected correlations between these structural and biochemical vegetation traits and PFTs. This made the functional response of the vegetation community (community level PFTs) detectable in the spectral response and enabled us to model, predict and map a series of PFTs (plant life and growth forms, CSR strategy types, indicator values). We illustrate the connections between the functional and spectral response of the vegetation community via their links to spectrally detectable vegetation traits in a framework merging theory and concepts of imaging spectroscopy and vegetation ecology. We attribute the successful determination of this broad range of vegetation characteristics in a topographically and ecologically challenging environment mainly to our sampling design, which was apparently able to capture enough of the study area's heterogeneity. Given the difficulties of traditional vegetation ecological field surveys in remote, heterogeneous and sensible areas, imaging spectroscopy offers the chance to collect relevant vegetation data needed to address today's most pending environmental issues on a large scale. There is general agreement on the usefulness of PFTs to assess ecosystem processes and services (Smith *et al.* 1997; Ustin & Gamon 2010; Lavorel 2013) and their links to abiotic and biotic environmental factors allow them to be integrated in globally coherent assessment schemes (Reich *et al.* 1999; Wright *et al.* 2004). However, there are likely no universally indicative vegetation traits or PFTs (Gitay & Nobel 1997). In some instances, simplistic structural and biochemical vegetation traits (such as vegetation quantity and quality) might be equally or even more relevant compared to PFTs, as we show with our analysis of ungulate movement patterns. Thus, the use of vegetation traits and PFTs as indicators for ecosystem processes and services has to be based on ecological knowledge and the context of the study (Kattge *et al.* 2011).

This thesis provides an example of how interdisciplinary research can promote scientific advancement, as well as public awareness and support. Combining theory and methods from imaging spectroscopy and vegetation ecology opened up a set of scientific questions to more detailed investigations. Since decades researchers in the Swiss National Park were interested in how patterns of chemical and functional vegetation composition influence and get influenced by the animal community (e.g. Schütz *et al.* 2003; Suter *et al.* 2004; Risch *et al.* 2008; Schütz *et al.* 2014). However, the lack continuous environmental data and the problem of model extrapolations in a highly heterogeneous landscape limited these studies to small areas. Likewise, understanding of how vegetation patterns change after human land use in the form agriculture, forestry and mining had stopped was already a central goal

for researchers during the founding process of the Swiss National Park in the early 20th century (e.g. Kupper 2009). Now, vegetation patterns can be investigated continuously, at high spatial resolution and studies are no longer limited to a number of research plots but can cover the entire area of the Swiss National Park and neighbouring regions. Disentangling the effects of current and historic human influence, biotic and abiotic factors on vegetation patterns is particularly important in the view of the anticipated climatic changes in Alpine regions (Theurillat & Guisan 2001).

Conducting this thesis at three research institutions, the Remote Sensing Laboratories (RSL) of the University of Zurich, the Swiss Federal Institute of Forest, Snow and Landscape Research (WSL) and the Swiss National Park (SNP), provided numerous opportunities for presenting concepts, techniques and results not only to a broad range of scientists from various fields, but also to the broader public, e.g. school classes, students from different faculties of several countries, politicians, conservation groups, national park guests, and the local population of the Engadin. This research excited many and promoted the fascination for nature, but also increased awareness of environmental challenges and, most importantly, pointed out how research and technology are currently used to investigate and monitor some of today's most pending global issues, such as species and habitat loss, nutrient deposition and land use change (MEA 2005). Although the research for this thesis was carried out in a relatively small area with very distinctive characteristics, the methods developed can be extended to other study areas, larger geographic regions and measurement taken by different instruments. Given the challenges imposed by rapid and accelerating global change, interdisciplinary research teams enabling scientific exchange, cooperation and understanding across fields and promoting public outreach are crucially needed. This thesis shows how placing scientific concepts into broader contexts and consolidating the jargon of different research areas can advance scientific cooperation, create products of wide applicability and multiply public awareness and support by making science better understandable.

5.3 Outlook

The aims of the research conducted in this thesis were to explore the use of imaging spectroscopy for ecological applications in a highly heterogeneous alpine grassland system. Using data from the airborne imaging spectrometer APEX we were able to accurately model and predict various vegetation traits, i.e. plant biomass, plant N, plant NDF content, plant strategy types, indicator values, plant life and growth forms. This enabled us to produce a series of resource maps with 2 x 2 m spatial resolution that are now available via the SNP's Research and Geoinformation Department. These data shall contribute to various research projects and serve as a baseline against which to assess future changes regarding ecosystem processes and services or species distributions. As data continuity is a prerequisite for separating long term patterns from inter-year variability, which is assumed to be considerable in alpine environments, we strongly encourage continuation of imaging spectrometer flights of APEX or a comparable sensor. A possible sampling scheme could consist of four flights during four consecutive years carried out every 10-15 years, as it was started in the preparation phase of this thesis in 2010.

After demonstrating the use of resource maps for investigating the foraging behaviour of ungulates, in a next step one could envisage combining indicators for vegetation quantity and quality in combination with predictive modelling of animal behaviour. Resource partitioning has been an issue of concern for a long time, and spectroscopy based approaches allow to derive those resources from a continuum (Prins & Fritz 2008). In particular, distinguishing between accessible and non-accessible resources will further help to differentiate resource partitioning beyond the classical land cover based

or even continuous field approaches (Mutanga & Skidmore 2004; Skidmore *et al.* 2010). Recombined multiple continuous fields of vegetation quantity and quality could further help to investigate resource allocation (Kneubühler *et al.* 2014). Moreover, linking multi-temporal resource maps with the habitat use patterns of individual animals and their lifetime reproductive success would enable to investigate different life-history strategies and their fitness consequences (e.g. investing in offspring vs. individual lifetime; McLoughlin *et al.* 2007; Losier *et al.* 2015). Given a high enough temporal resolution, resource maps could also be used to investigate the triggers for other behaviours, such as seasonal migration patterns (McNaughton 1988; Albon & Langvatn 1992; Müller *et al.* 2008).

Currently, we investigate the possibility for temporal extrapolations of imaging spectroscopy data using field spectrometer measurements (Utzinger 2015). APEX data are being combined with field spectroscopy data collected at the time of the APEX overflight (July) to extrapolate two additional field spectrometer data sets collected in June and August to the level of APEX measurements, with the ultimate aim to produce synthetic APEX images for these two additional months (Fig. 5.1). Synthetic APEX images would provide great additional value, as they could be created on demand involving relatively little cost and time.

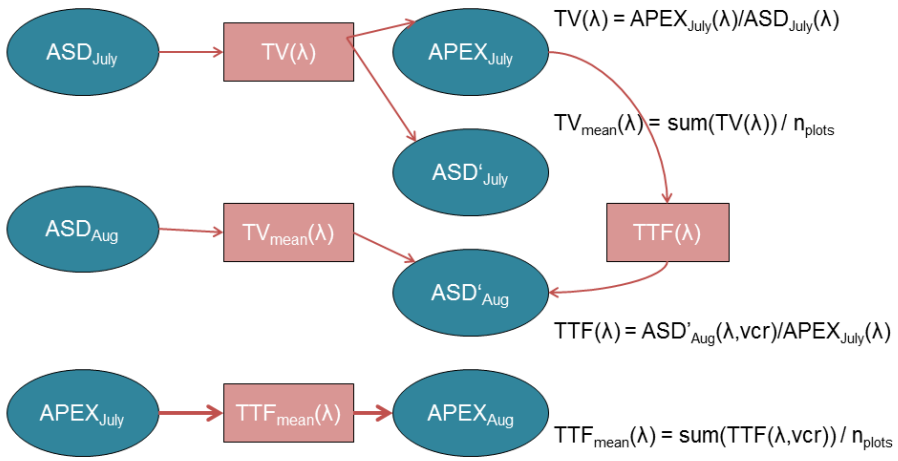

Figure 5.1 Workflow for creating synthetic APEX imagery. Wavelenght (λ) dependent transformation vectors (TV) extrapolate field spectrometer data (ASD_{July}, ASD_{Aug}) to the level of APEX imaging spectrometer data (ASD'_{July}, ASD'_{Aug}). Comparing ASD'_{Aug} with the original APEX data ($APEX_{July}$) enables determining the time-transformation function (TTF) for developing synthetic APEX images ($APEX_{Aug}$; diagram developed by A. Hueni, F. Utzinger and A.K. Schweiger).

Furthermore, we plan to improve our biomass models for predicting and mapping PV and NPV combined, based on a spectral library of pure PV and NPV end-members collected using a field spectrometer. NPV, consisting predominantly of plant litter, is the main material processed by above-ground and below-ground microbial communities and thus central to biogeochemical cycling in grasslands (Leuschner 2005). Moreover, plant litter is the most important component of the fuel load in grassland ecosystems (Leuschner 2005). In the past, natural wildfires exerted a major control over the SNP´s ecosystems, resetting the vegetation community on a cyclic basis every 250 to 600 years (Stähli *et al.* 2006). These recurring fire regimes presumably enabled not only the mountain pine (*Pinus mugo ssp. uncinata*) forests to persist, but were likely equally important for establishing and maintaining the biodiversity in the SNP's alpine grasslands by, depending on the disturbance extent, triggering patch dynamics or cyclic succession (van der Maarel 2005). Thus, studying plant litter distribution with NPV models could reveal insights into the importance of fire regimes for ecosystem dynamics in grasslands.

Another perspective involves using APEX data to model, predict and map the distribution of vegetation characteristic indicating former land use practices in the SNP. Tall-herb/meadow communities can, for example, still be found around the abandoned stables and on former cattle resting places where high input of cattle excreta enriched soil nutrient concentrations (Schütz *et al.* 2006). One particular vegetation community dominated by the *Aconitum napellus* L. agg., indicative for such cattle resting places, seems to exhibit distinct optical characteristics and was already qualitatively detected using APEX data (Fig. 5.2). In the future, we will include optical characteristics of further indicative vegetation communities to model former land use practices and use historic maps for model validation.

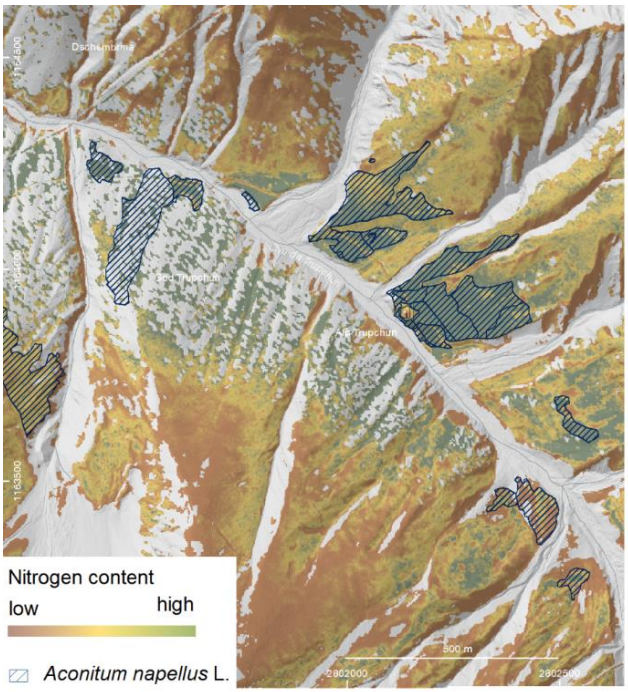

Figure 5.2 Distribution of *Aconitum napellus* L. agg. colonies and their correlation with plant nitrogen content (Schütz & Risch 2013).

5.4 Future directions

The research conducted in this thesis has pointed out the potential for many ecological applications of imaging spectroscopy. Given the global dimensions of today's biggest environmental threats, resource degradation and changes to the biogeochemical cycle (Leuschner 2005), 'ecological remote sensing' needs to be brought to the global scale. The expected launches of the spaceborne imaging spectrometers EnMAP (planned in 2017; Kaufmann *et al.* 2013), PRISMA (planned in 2017; Lopinto & Ananasso 2013), and HyspIRI (expected after 2022; NASA 2012) will boost the opportunities for global approaches. To fully exploit these opportunities, multidisciplinary research teams, involving remote sensing scientists and ecologists from different fields (vegetation, animal, soil and microbial ecology) are needed. Joint research structures will enable the incorporation of the expertise of scientists from different regions of the world and global databases will provide the large data collections needed for identifying general ecosystem responses (van der Meer *et al.* 2009) and developing coherent assessment and monitoring schemes.

5.4.1 Linking plant functional and spectral types to ecosystem services

Defining the relevance of different ecosystem services for a given landscape, linking these services to measurable traits of organisms and understanding the physiological function of these traits are major tasks for the scientific community (Gitay & Nobel 1997; Ustin & Gamon 2010; Andrew *et al.* 2014). Additionally, characterizing tolerance limits of single species and distinguishing between ubiquitous and differential species, with the latter most useful for ecosystem service assessment, is a topic of ongoing research (Austin 2005). Often, integrating the characteristics of several species and using communities as indicators is advantageous as the overlap of ecological tolerances of many species is smaller than the ecological amplitude of a single species (Diekmann 2003). Moreover, turnover rates of individuals and species can be fast, due to cyclic changes caused by the death of individuals or small scale disturbances (gap dynamics), while the vegetation community might remain relatively stable and thus more reliably indicating the buffer capacity of ecosystems (Leuschner 2005). As roles and functions of plants can be linked to investment or life history strategies, which are in turn reflected by structural and chemical traits (Lavorel *et al.* 1997; Tilman *et al.* 1997) and follow surprisingly consistent global patters (Reich *et al.* 1992; Wright *et al.* 2004), PFTs allow for the generality and causality needed for global ecosystem service assessment (McGill *et al.* 2006).

Plant functional types can be identified subjectively (e.g. life and growth forms), deductively based on a-priori statements of their importance (e.g. keystone species) or based on data-driven approaches, such as multivariate cluster techniques (e.g. CSR strategy types; Gitay & Nobel 1998). To be useful for ecosystem service assessment, the species groups should show similar responses and similar response mechanisms to a syndrome of environmental factors (i.e. a combination of biotic and abiotic processes that change due to perturbations; Gitay & Nobel 1998). Plant functional types defined in this way can be directly used for indication, as their response (their presence or absence, abundance, state) is causally linked to specific ecosystem properties, which can be defined based on the processes of interest.

For global ecosystem service assessment PFTs not only have to be linked to ecosystem functions and processes, they also need to be detectable and thus causal relationships between PFTs and the spectral response have to be established (Ustin & Gamon 2010). If these links can be established and structural and biochemical traits are detectable with imaging spectroscopy, the use of 'optical types', i.e. optically distinguishablePFTs, could be feasible (Ustin *et al.* 2004; Aplin 2005; Kokaly *et al.* 2009; Ustin & Gamon 2010). In analogy to the niche theory, optical types are located in an n-dimensional hyper-volume, with multidimensional axes corresponding to the spectral signatures of optically detectable structural or biochemical traits (Ustin & Gamon 2010). For example, as the main CO_2-fixing enzyme involved in photosynthesis RuBisCO (Ribulose-1,5-bisphosphate carboxylase-oxygenase) accounts for 30 to 60% of the total N content in plants (Elvidge 1990), net photosynthetic capacity is directly linked to plant N content (Reich *et al.* 1999), which is known to be detectable in the spectral signature of vegetation (Kokaly *et al.* 2009). Likewise, the leaf-area index (LAI) is positively linked to net photosynthetic capacity and can be spectrally detected (Ollinger 2011). Therefore, an optical type for net photosynthetic capacity, with axes corresponding to the spectral signatures of plant N content and LAI, could be definable, given that the data collected covers the entire expected variability for the system of interest (Asner *et al.* 2011).

While there is considerable knowledge about the influences of pigments in the VIS and water absorption features in the NIR and SWIR, far less is known on the influences of structural plant components in the NIR part of the spectrum (Ollinger 2011). Additionally, many studies focused on investigating the causal links between plant traits and the spectral response at the leaf scale (Asner *et*

al. 2014; Serbin *et al.* 2014), while far less is known at canopy and stand scales, which are particularly important when using airborne and satellite data. However, some level of convergence between plant structural traits and the spectral response at multiple scales, from the leaf, to the canopy and stand scale was already detected (Ollinger 2011). Generally, plants in resource poor environments have low photosynthesis rates and thus low levels of plant N. At the leaf scale, low N levels are functionally coupled to more densely packed cell structures (detectable via low reflectance values in the NIR), resulting in low rates of CO_2 diffusion to the chloroplasts and more vertically orientated leaves; at the canopy scale, low N levels reduce stem elongation and crown diameter resulting in more densely clustered leaves along the stem; and at the stand scale, plants in resource poor environments populate the landscape in a more scattered fashion (Ollinger 2011). Thus, plants in N limited environments generally exhibit greater clumping of different functional traits compared to resource rich environments and these effects become apparent at different scales, pointing towards an optimization of plant form associated with plant function at multiple levels (Ollinger 2011). Such correlations between structural vegetation traits and the spectral response at multiple levels could link canopy spectra to plant function in a similar way as leaf spectra. However, more research is needed to support this idea. Additional insights into possible convergence between structural vegetation traits at multiple levels will likely be gained, when combining imaging spectroscopy data with high spatial resolution LIDAR (light detection and radar) data (Asner & Martin 2008).

5.4.2 Assessing diversity using imaging spectroscopy

The abundance, density and diversity of organisms constitute the composition, structure and functioning of ecosystems, making biodiversity an underlying necessity for the provisioning of ecosystem services (MEA 2005). This recognition resulted in a research focus on global diversity assessment and monitoring. As an emergent property of ecosystems, diversity influences ecosystem functioning and persistence, but the role of diversity cannot be fully interfered from the species level alone (Leuschner 2005). While the presence and absence of specific species can indicate relevant changes to ecosystems (Kurokawa *et al.* 2010; van Kleunen *et al.* 2010), changes in species composition can alter ecosystem processes even if the number of species present remains unchanged or increases (MEA 2005). Thus, measures of diversity involving the absolute number of species only, either within (α diversity) or between communities (β diversity), or at the landscape level (γ diversity), are not necessarily indicative for ecosystem functioning. In natural communities, diversity depends on evolutionary and ecological processes, such as speciation, adaption and extinction, which all effect ecosystem functioning (Lepš 2005). Some of the world's oldest and most extensive ecosystems contain few species and there is no clear evidence that ecosystem processes depend on higher levels of diversity (Grime 1997). While in some ecosystems productivity (Tilman *et al.* 2001) or stability (Tilman *et al.* 2006) might depend on high levels of diversity, in other ecosystems the situation can be reversed (Wardle *et al.* 1997). It likely is the particular composition of species, rather than absolute numbers, together with the specific ecosystem conditions, as influenced by nutrient availability, herbivory and soil biota, that causes relationships between diversity and ecosystem functioning. Additionally, diversity should be investigated together with evenness (Mulder *et al.* 2004; Lepš 2005), the different abundances of species within different communities, but again no general rule for the relationship between evenness and ecosystem functioning should be expected. Although abundant (dominant) species are assumed to have greater influence on ecosystem functioning than less abundant species, following the mass ratio hypothesis of Grime (1998), plant species with low abundances can be crucial for the persistence of specialized microbial, animal or other plant

communities (Lepš 2005) which could in turn influence ecosystem functioning. As the relationships between diversity and ecosystem function depend on the ecological attributes of the species present (Wardle *et al.* 1997), the focus of diversity assessments should be laid on identifying the irreplaceable species (so-called keystone species) and functional types (Grime 1997).

A promising approach to assess diversity on the species level is provided by the airborne spectranomics framework (Asner & Martin 2008). As chemical and spectral diversity have been shown to increase with species diversity, the spectral response of the vegetation community can be used to calculate species diversity indices (Asner & Martin 2008; Asner *et al.* 2014). Moreover, spectra from individual species, transferred to the leaf level using inverted radiative transfer models (RTMs), can be converted into chemical fingerprints, used as input into spectral libraries and matched to the chemical signatures of PFTs, plant families and possibly also individual species (Asner & Martin 2008). Additionally, future research will go beyond species diversity and includes other aspects of diversity important for ecosystem functioning, e.g. functional (Díaz & Cabido 2001; Mokany *et al.* 2008; Asner *et al.* 2014) and phylogenetic diversity (Cadotte *et al.* 2009; Madritch *et al.* 2014).

The increasing data availability from operational satellite programs and easily accessible global databases can be expected to encourage comparative studies and the definition of guidelines on which functional types and diversity indices to use as indicators for assessing ecosystem processes and services. Finally, simulation models combining global functional and diversity data sets with climatic, demographic and socioeconomic data will then enable to quantify the responses of ecosystem functions to management decisions, to test the sensitivity of ecosystems to individual drivers or to future climate and land use change scenarios and thus to predict long term consequences of altered ecosystem condition, including trade-offs between different processes and services (MEA 2005).

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CURRICULUM VITAE

ANNA-KATHARINA SCHWEIGER

Research interests

- Ecosystem ecology
- Vegetation ecology
- Movement ecology
- Remote sensing
- Community ecology
- Conservation

Education

2012 – 2015	PhD in Geography. University of Zurich, Remote Sensing Laboratories. Swiss Federal Institute for Forest, Snow and Landscape Research WSL. Swiss National Park. Thesis: "Ecological applications of imaging spectroscopy in alpine grasslands". Focus: grassland ecology, imaging spectroscopy, movement ecology.
2010	MSc in Wildlife Ecology and Wildlife Management. University of Natural Resources and Applied Life Sciences Vienna. Thesis: "Accounting for interaction terms in logistic regression analysis: Summer habitat use of rock ptarmigan and black grouse in the Austrian Alps". Focus: habitat modeling, endangered, protected, invasive and recovering species, population dynamics, monitoring concepts, stakeholder communications.
2007	BSc in Biodiversity and Ecology. University of Graz. Thesis I: "Environmental and Landscape Protection in Agriculture". Thesis II: "Aquatic Ecology and Water Engineering". Focus: plant and animal systematics, morphology, physiology, community ecology, aquatic ecology, environmental protection.

Professional appointments

05/2015 – present	Postdoctoral Associate, University of Minnesota - Saint Paul, Department of Ecology, Evolution & Behavior, Cavender-Bares Lab. Main project: "Dimensions of Biodiversity - Linking remotely sensed optical diversity to genetic, phylogenetic and functional diversity to predict ecosystem processes".
12/2011 – 05/2015	Research Fellow. Research and Geoinformation Department, Swiss National Park. Focus: research coordination, databank management, data analysis, monitoring (ungulates, birds, fish), supervision of interns.
05/2011 – 11/2011	Internship. Swiss National Park. Focus: fieldwork for imaging spectrometer flights, analyses of vegetation samples, field assistance SNF project "Trophic cascades: The effects of herbivory on grassland ecosystems", ungulate monitoring.
10/2010 – 04/2011	Internship. Swiss Federal Institute for Forest, Snow and Landscape Research (WSL). Focus: laboratory near-infrared spectroscopy (soil, vegetation), fibre and nutrient analysis (vegetation), sample collection and processing (soil, vegetation).

03/2010 – 09/2010	Internship. Swiss National Park. Focus: research proposal "Resource selection of wild ungulates in an unmanaged habitat", ungulate monitoring, marking and radio-collaring.
11/2008 – 01/2010	Research Assistant. "The impact of elevated cables (chairlifts) on grouse mortality", University of Natural Resources and Applied Life Sciences Vienna.
08/2009	Research Assistant. Monitoring of small mammals, University of Natural Resources and Applied Life Sciences Vienna.
06/2009	Research Assistant. Annual census of ground squirrels, Union for Nature Preservation in Lower Austria.
06/2008 – 06/2009	Research Assistant. Annual census of rock ptarmigan, University of Natural Resources and Applied Life Sciences Vienna.

Publications ISI

- Anderwald P., Herfindal, H., Haller, R.M., Risch A.C., Schütz, M., Schweiger, A.K. & Filli, F. (2015). Influence of migratory ungulate management on competitive interactions with resident species in a protected area. Ecosphere (accepted).
- Fatehi P., Damm A., Schweiger A.K., Schaepman M.E. & Kneubühler M. (2015). Mapping alpine aboveground biomass from imaging spectrometer data: a comparison of two approaches. IEEE Journal of Selected Topics in Applied Earth Observations and Remote Sensing, 8:3123-3139.
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- Anderwald P., Haller R., Risch A.C., Schütz M., Schweiger A.K., Filli F. (2013). Resource competition between chamois, alpine ibex and red deer in the Swiss National Park? In: 5th Symposium for Research in Protected Areas; Mittersill, Austria, June 10-12, 2013. http://www.landesmuseum.at/pdf_frei_remote/NP-Hohe-Tauern-Conference_5_0015-0018.pdf
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- Schweiger, A.K., Zohmann, M. (2009). Small-scale habitat use of Black Grouse (Tetrao tetrix) in the Austrian Alps. In: Polish Society for Birds Protection, 5th European Conference - Black Grouse-Endangered Species, Białowieża, Poland, October 5-9, 2009.
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Other Publications

- Meier A., Olff, S.(2014). Huftiere im Schweizerischen Nationalpark (Documentary). 3sat Nano, September 24, 2014. http://www.3sat.de/mediathek/?mode=play&obj=46241
- Schweiger A.K. (2014). Neue Erkenntnisse aus der Forschung: Moderne Fernerkundung von Huftierarten in der Val Trupchun, Contribution of the Academia Raetica. In: Bündner Woche, July 16, 2014.
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- Schweiger A.K., Rapp M., Kneubühler M. & Risch A.C. (2013). Bildspektrometrie im SNP. Ökologie trifft Fernerkundung. In: Atlas des Schweizerischen Nationalparks. Die ersten 100 Jahre. Nat.park-Forsch.Schweiz 99/1 (eds. Haller H, Eisenhut A & Haller R). Haupt Verlag, Bern, pp. 190-191.
- Wartmann B. & Schweiger A.K. (2013). Orchideen. Erste Ergebnisse systematischer Kartierung In: Atlas des Schweizerischen Nationalparks. Die ersten 100 Jahre. Nat.park-Forsch.Schweiz 99/1 (eds. Haller H, Eisenhut A & Haller R). Haupt Verlag, Bern, pp. 98-99.

Supervision

2015	Fiona Utzinger, "Creation of synthetic imaging spectroscopy time series from airborne and ground based spectral data", University of Zurich, Remote Sensing Laboratories, MSc thesis.
2013	Maia Rapp, "Biomass-mapping of alpine grassland with APEX imaging spectrometry data", University of Salzburg, Department of Geoinformatics UNIGIS, MSc thesis.

Grants, awards

2013	University of Natural Resources and Applied Life Sciences Vienna, Granser United Global Academy Award.
2009	University of Natural Resources and Applied Life Sciences Vienna, scholarship.
2008	University of Natural Resources and Applied Life Sciences Vienna, research grant: "Summer habitat use of rock ptarmigan and black grouse in the Austrian Alps".
2008	University of Natural Resources and Applied Life Sciences Vienna, scholarship.

Reviewer for journals

- Ecological Applications
- International Journal of Remote Sensing
- Mammalian Biology
- Journal of Ornithology
- European Journal of Wildlife Research

Graduate courses and professional training

- Data analysis with R
- Data analysis in vegetation ecology using R
- Movement ecology
- Animal movement ecology summer school
- Adobe InDesign basics
- Fund acquisition for researchers
- Negotiation and moderation techniques
- Effective scientific presentations
- Principles and theories in geography
- PhD seminar I & II
- Graduate school retreat I & II

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